On kannemeyeriiform dicynodonts from the Shaanbeikannemeyeria Assemblage Zone of the Ordos Basin, China postprint

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Abstract

Shaanbeikannemeyeria is a common tetrapod from the lower part of the Ermaying Formation of the Ordos Basin, China. There are taxonomical questions surrounding this genus, such as the validity of the genus, and how many species are included within it. Several specimens have been collected since 1978. Shaanbeikannemeyeria first appeared from the top of the Heshanggou Formation. These specimens are described to clarify the diagnostic characters, the individual variations and the phylogenetic position of Shaanbeikannemeyeria. Only one species, S. xilougouensis, is recognized. It is characterized by the following autapomorphies: occiput strongly inclined relative to the palate such that the skull is much shorter basally than dorsally, sword tip-like premaxillary posterodorsal processes, tall and dorsally-convex cutting blade on the medial edge of the dorsal surface of the dentary, reflected lamina with a separated posteroventral process, and 15 dorsal vertebrae. This species shows variations on the cranial morphology, such as the occiput height relative to the width, the snout tip (sharp or obtuse), the shape of the orbital portion of the zygomatic arch, and the shape of caniniform process. Some variations could be ontogenetically related, such as the development of the caniniform process and tusk, the posterior extension of the maxilla on the zygomatic arch, the distance between the frontal and the premaxilla, the intertemporal bar width, and the exposing degree of the parietals. Based on postcranial bones, the second dicynodont genus (possibly Parakannemeyeria) is present in the lower Ermaying Formation.

Full Text

Preamble

On kannemeyeriiform dicynodonts from the Shaanbeikannemeyeria Assemblage Zone of the Ordos Basin, China

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Abstract

Shaanbeikannemeyeria is a common tetrapod from the lower part of the Ermaying Formation of the Ordos Basin, China. Taxonomic questions surrounding this genus include its validity and the number of species it contains. Several specimens have been collected since 1978, with the genus first appearing at the top of the Heshanggou Formation. These specimens are described herein to clarify diagnostic characters, individual variation, and phylogenetic position. Only one species, *S. xilougouensis*, is recognized, characterized by the following autapomorphies: occiput strongly inclined relative to the palate such that the skull is much shorter basally than dorsally; sword tip-like premaxillary posterodorsal processes; tall and dorsally-convex cutting blade on the medial edge of the dorsal surface of the dentary; reflected lamina with a separated posteroventral process; and 15 dorsal vertebrae. This species shows variation in cranial morphology, including occiput height relative to width, snout tip shape (sharp or obtuse), shape of the orbital portion of the zygomatic arch, and shape of the caniniform process. Some variations appear ontogenetically related, such as development of the caniniform process and tusk, posterior extension of the maxilla on the zygomatic arch, distance between the frontal and premaxilla, intertemporal bar width, and degree of parietal exposure. Based on postcranial bones, a second dicynodont genus (possibly *Parakannemeyeria*) is present in the lower Ermaying Formation.

Key words: Heshanggou Formation, Ermaying Formation, Middle Triassic, Anisian, Kannemeyeriiformes

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1 Introduction

During 1962–1964, Cheng Zhen-Wu from the Institute of Geology, Chinese Academy of Geological Sciences (IGCAGS) collected numerous Permo-Triassic vertebrate fossils from the Ordos Basin. Based on these materials, he established several new taxa, including *Shaanbeikannemeyeria xilougouensis* from Fugu County, Shaanxi Province (Cheng, 1980). In 1976 and 1977, the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences (IVPP) sent a field team to Junger Banner, Nei Mongol, where they discovered fossil-bearing layers from the Heshanggou Formation and the lower part of the Ermaying Formation that yielded a diverse tetrapod fauna. An incomplete skeleton from Buerdong (locality 76014) was referred to *Shaanbeikannemeyeria* as the holotype of *S. buerdongia* (Li, 1980), though it has recently been regarded as a junior synonym of *S. xilougouensis* (Li and Liu, 2015). In the Gucheng-Buerdong area, *Shaanbeikannemeyeria* is the only known dicynodont from the lower Ermaying Formation; however, approximately 100 km south of this area, *Parakannemeyeria xingxianensis* was reported from the lower Ermaying Formation (Cheng, 1980).

Shaanbeikannemeyeria is a common tetrapod within the fossil-bearing strata, and tetrapod assemblage zones have been named based on this genus (Li and Cheng, 1995; Liu, 2018). Nevertheless, several questions about this genus remain unresolved. The validity of *Shaanbeikannemeyeria* has been questioned, with proposals that it is synonymous with *Kannemeyeria* (King, 1988; Lucas, 2001) or congeneric with *Rechnisaurus* (Cox, 1991). Although recent researchers have accepted its validity, no consensus has been reached regarding its phylogenetic position. It was initially proposed as the sister taxon of *Kannemeyeria* (Kammerer et al., 2013), but more recently has been viewed as an early-diverging clade of Kannemeyeriiformes (Angielczyk et al., 2017; Kammerer et al., 2019; Kammerer and Ordoñez, 2021). The stratigraphical distribution of *Shaanbeikannemeyeria* also requires clarification.

During 1978–1980, IVPP teams collected three specimens of *Shaanbeikannemeyeria* from Fugu, Shaanxi and Junggar, Nei Mongol. In 1988 and 1997, additional kannemeyeriiform specimens were collected by teams led by Li Jin-Ling. These specimens are described here to clarify the distribution, diagnosis, variation, and phylogenetic position of *Shaanbeikannemeyeria*. Furthermore, the presence of a second dicynodont genus is confirmed from the lower Ermaying Formation.

2 Geological Setting

The fossils were collected from a small area near the border between Shaanxi and Nei Mongol, corresponding to Fugu County and Junger Banner respectively. Most specimens derive from the lower Ermaying Formation, except for one (IVPP V 11675) from the top of the Heshanggou Formation. A stratigraphic column was measured at Fugu in 1997 and 1998, with fossil horizons marked [Figure 1: see original paper]. The lower Ermaying Formation from Liulin, more than 200 km to the south, has been dated as Anisian in age (Liu et al., 2018).

3 Materials

Numerous kannemeyeriiform specimens were collected. Examined specimens are listed in Table 1 . All listed specimens can be referred to *S. xilougouensis* except for IVPP V 30727 and V 30730, which are tentatively identified as *Parakannemeyeria*.

Anatomical abbreviations: acd, anterior condyle; act, acetabulum; An, angular; ap, anterior process; apr, anterior palatal ridge; Ar, articular; As, astragalus; Bo, basioccipital; bt, basal tuber; Ca, calcaneum; cap, capitulum; cen, centrum; cd, condyle; ch, choana; cnc, cnemial crest; co, crista oesophagea; cp, caniniform process; cr, cervical rib; D, dentary; d1–5, digital 1 to 5; do, dorsal opening of interpterygoid vacuity; dpc, deltopectoral crest; dr, dorsal rib; dt, distal tarsal; dv, dorsal vertebra; Ec, ectopterygoid; ect, ectepicondyle; ent, entepicondyle; entf, entepicondylar foramen; Ep, epipterygoid; epu, for epipubis; F, frontal; Fe, femur; Fi, fibula; fm, fenestra magnum; fo, fenestra ovalis; f.pap, facet for paroccipital process; f. qp, facet for quadrate ramus of pterygoid; f.s, facet for stapes; Hu, humerus; ic, internal carotid canal; IL, ilium; ipv, interpterygoid vacuity; Is, ischium; J, jugal; jf, jugular foramen; L, lacrimal; la, lacrimal foramen; ld, insertion of M. latissimus dorsi; lds, lateral dentary shelf; lf, labial fossa; lpf, lateral palatal foramen; M, maxilla; mf, mandibular fenestra; mpr, median palatal ridge; mt, metatarsal; n, naris; N, nasal; ns, neural spine; oc, occipital condyle; of, obturator foramen; olf, olecranal facet; P, parietal; pap, paroccipital process of opisthotic; Pbs, parabasisphenoid; pcd, posterior condyle; Pe, periotic; Pf, prefrontal; pf, pineal foramen; Pl, palatine; Pm, premaxilla; Po, postorbital; Pop, postparietal; poz, postzygapophysis; Pp, preparietal; Pra, prearticular; prz, prezygapophysis; Pt, pterygoid; ptf, posttemporal fenestra; Pu, pubis; Q, quadrate; Qj, quadratojugal; qrp, quadrate ramus of pterygoid; Ra, radius; rl, reflected lamina of angular; Sa, surangular; scs, insertion of M. subcoracoscapularis; Sm, septomaxilla; So, supraoccipital; Sp, splenial; Sq, squamosal; sr, sacral rib; St, stapes; st, sella turcica; sup, supinator process; sv, sacral vertebra; T, tabular; t, tusk; Ti, tibia; tp, tympanic process; tr, trochlear; trm, trochanter major; u, ungual; Ul, ulna; V, vomer; wf, wear facet.

Table 1. List of studied specimens in this paper

Specimen	Skull	Skull basal length	Lower jaw	Postcranial bones	Notes
Shaanbeikannemeyeria					
adult IGCAGS V315[1]	nearly complete	27 cm	absent	absent	holotype of *S. xilougouensis*

Specimen	Skull	Skull basal length	Lower jaw	Postcranial bones	Notes
IVPP V 6033[2]	incomplete	31 cm	present	left humerus	holotype of *S. buerdongia*
IVPP V 11674	nearly complete	24 cm	present	scapula, humerus, clavicle	neotype
IVPP V 11675	incomplete	~27 cm	present	absent	
IVPP V 11677	incomplete	29 cm	present	absent	
subadult IVPP V 11676	16 cm	present	absent		
IVPP V 17904	~21 cm	present	absent		
IVPP V 30725	~14 cm	present	absent		
IVPP V 30726	~18 cm	present	partial skeleton		
juvenile IVPP V 30729*	<10 cm	present	absent		
?Parakannemeyeria					
IVPP V 30727	absent	absent	present		
IVPP V 30730*	absent	absent	present		

[1] holotype of *S. xilougouensis*; [2] holotype of *S. buerdongia*; * found in association

4 Systematic Palaeontology

Anomodontia Owen, 1860
Dicynodontia Owen, 1860
Dicynodontoidea Olson, 1944
Kannemeyeriiformes Maisch, 2001
Shaanbeikannemeyeria xilougouensis Cheng 1980

Holotype: IGCAGS V315, a nearly complete skull.

Neotype: IVPP V 11674, a nearly complete skull with lower jaw.

Type locality and horizon: Xilougou, Gucheng Township, Fugu County, Shaanxi Province, China; base of Ermaying Formation.

Referred specimens: IVPP V 6033, V 11676, V 11677, V 17904, V 30725, V 30726, V 30728, and V 30729, lower Ermaying Formation; V 11675, Heshanggou Formation.

Revised diagnosis: Medium-sized kannemeyeriiforms with the following autapomorphies: occiput strongly inclined relative to the palate such that the skull is much shorter basally than dorsally; sword tip-like premaxillary posterodorsal processes; tall and dorsally-convex cutting blade on the medial edge of the dorsal surface of the dentary; reflected lamina with a separated posteroventral process; and 15 dorsal vertebrae.

Differentiated from *Uralokannemeyeria* by postorbital that does not extend the entire length of the intertemporal bar, and an oblique ridge on the lateral side of the zygomatic arch in adults; differentiated from *Rechnisaurus* by lacking deep depressions lateral to the midline ridge on the snout; differentiated from *Kannemeyeria* by having the anterior tip of snout squared off, notch absent on the dorsal edge of narial opening, parietals exposed in the midline groove, and a median pterygoid plate with a thin median ridge on the ventral surface. Differentiated from *Shansiodon* by its larger size, relatively small temporal fenestrae, intertemporal bar that is wide, not crest-like, and raised from the skull roof; differentiated from *Sinokannemeyeria* and *Parakannemeyeria* by short snout, premaxillary lateral surface anterior to the external naris without lateral extension, small caniniform process and tusk, narrower interorbital region, and longer intertemporal bar.

5 Description

Known specimens vary in size (Supplementary file 1). The maximum known skull length (from snout tip to posterior edge of squamosals) is 42 cm (holotype), with maximum occipital width of ~40 cm (holotype), while the smallest specimen has an estimated skull length of 12 cm (IVPP V 30729). The skull and lower jaw of each specimen are described separately, while postcranial bones are described together. The skull of IGCAGS V315 and lower jaw of IVPP V 11674 are described in detail, with other skulls and lower jaws highlighting important similarities and differences.

5.1 Skull and Lower Jaw

IGCAGS V315. The skull is nearly complete, missing only the quadrate and quadratojugal complexes, and the left postorbital. No lower jaw is preserved. It was described and figured by Cheng (1980) [Figure 2: see original paper]. This specimen was stored at IGCAGS but can no longer be traced. The following description is based on observations made before its loss and on Cheng's original description (1980).

The skull is nearly triangular in dorsal view, not accounting for the occiput. Its occiput is strongly inclined posteriorly such that the skull is much shorter basally than dorsally and relatively low. In lateral view, the skull anterior to the temporal fenestrae is strongly convex, with the peak on the nasals. The intertemporal bar extends posterodorsally, forming a 120° angle with the frontal.

The premaxilla has a wide anterior surface that forms a nearly right angle with the lateral surfaces, giving the anterior tip of the snout a squared-off profile [Figure 2: see original paper]. Posterodorsally, the two premaxillae first substantially shrink in width, then maintain this width for ~4 cm before rapidly converging at the midline to form sword tip-like processes between the nasals. The dorsal and lateral surfaces are covered by differently sized pits, indicating they were covered by a keratinous beak in life. The premaxilla has an obtuse anteroventral margin that nearly lies on a horizontal plane. Posteroventrally, the premaxillary ventral margin, together with the portion of maxilla anterior to the caniniform process, forms a nearly straight cut-edge [Figure 2C: see original paper]. On the palatal surface, the anterior ridges are paired and nearly parallel, also exposed in lateral view [Figure 2B: see original paper]. Posterior to them, a middle ridge slightly increases in width posteriorly and meets the blade-like mid-ventral plate of the vomer at the anterior margin of the choanae.

The external naris is elongated with no distinct notch on the dorsal edge. The embayment lies mainly below the naris, with a small postnarial portion. The external naris is surrounded by the premaxilla anteriorly, the nasal dorsally, and the septomaxilla ventrally. The septomaxilla lies above the maxilla and within the embayment of the external naris.

On the dorsal surface, a distinct median ridge increases in width upward and posteriorly from the ventral portion of the premaxilla to the anterior portion of the frontal. It measures 5 mm in width at the anterior tip but 35 mm on the frontal. Posteriorly, it continues as a narrow low ridge on the frontal and disappears anterior to the preparietal.

The maxilla has a short contact with the nasal dorsally and a straight suture with the premaxilla below the external naris. Posteriorly, it receives the anterior process of the squamosal laterally below the orbit and supports the jugal dorsally. The maxilla has a fat caniniform process that lies slightly below the anterior extended line of the zygomatic arch and can be observed in dorsal view. The surface of the caniniform process is rugose, while the maxillary lateral surface above is smooth. On the medial side, the caniniform process has a clear oblique furrow with the smooth maxillary palatal surface. Medial to this margin, a large labial fossa is formed by the maxilla, jugal, and palatine. The exposed tusks are short (47 mm) with sharp tips pointed anteroventrally. The tusk has a smooth wear facet on the medial side. The distance between the two tusks is 65 mm.

The two nasals occupy the largest area on the dorsal surface. They have a short posteromedial margin for the anteromedial process of the frontal and meet their counterpart on the midline. Their surface is rough, especially on the posterolateral side. The nasal boss is absent.

The ovoid orbit faces mainly laterally but also slightly anteriorly and dorsally. It is formed by the prefrontal and frontal dorsally, the lacrimal anteriorly, the postorbital posteriorly, and the jugal ventrally. The jugal forms the major part of the zygomatic arch but has narrow lateral exposure. On the ventral side, it extends anteromedially to contribute to the margin of the labial fossa. The zygomatic arch is robust, with its anterior (orbital) portion rod-like. The posterior portion is transversely expanded and has an oblique ridge on the lateral side, making it triangular in cross-section.

The triangular lacrimal is exposed anterior to the orbit on the lateral surface. Its anterior tip is close to but does not reach the septomaxilla. The rounded lacrimal foramen lies in a deeply concave area on the posterior ventral side of the bone. Above it lie a few narrow ridges. The lacrimal bulges laterally relative to the maxilla. It has a triangular ventral process overlapping the anterior process of the jugal on the orbital ventral margin.

The small prefrontal lies on the anterodorsal corner of the orbit and is mainly exposed on the dorsal surface. It extends only slightly beyond the orbital anterior margin and nearly aligns with the anterior extension of the frontal, but lies far behind the anterior extension of the lacrimal. Its suture with the lacrimal is unclear, but it is separated from the maxilla.

The two frontals have smooth surfaces and meet with a thin, low mid-ridge. Anteriorly, their short anteromedial processes insert between the nasals, while posteriorly they surround the preparietal and meet at the parietal. The frontal forms half of the orbital dorsal margin.

The postorbital forms the posterior margin of the orbit, the entire anterior margin, and most of the medial margin of the temporal fenestra. Its anterior portion is a wide strip that expands ventrally and overlaps the jugal laterally. It does not extend to the entire length of the intertemporal bar posteriorly, with the posterior portion of the intertemporal bar formed only by the parietals.

The preparietal lies in the concave area anterior to the pineal foramen and forms the anterior wall of the latter. The oval pineal foramen is a large, deep dorsal opening.

The parietals are well exposed on the intertemporal bar and raised as a nearly straight crest, similar to *Rhadiodromus* (Surkov, 2003). The two parietals meet along the midline to form a shallow groove. Posteriorly, they are separated by the postparietal on the skull roof and contact the squamosal laterally. The parietal and postorbital do not form a fossa on the ventral surface of the intertemporal bar.

The large temporal fenestra widens posteriorly. The squamosal constitutes the lateral and posterior margins of the temporal fenestra. It sends a long zygomatic process to contact the maxilla anterior to the postorbital bar [Figure 2C: see original paper]. Its zygomatic process decreases in height posterior to the postorbital bar and attenuates into a slice on the base in lateral view, but flares posteriorly with a wide base in dorsal view. In posterior view, the squamosal margin forms a distinct dorsolateral notch below the zygomatic arch [Figure 2D: see original paper]. The squamosal distinctly extends laterally, forming the lateral portion of the occiput. Dorsomedially, it contacts the parietal and postorbital on the anterior surface of the occiput, and the tabular and periotic on the posterior surface. It contributes to the lateral margin of the posttemporal fenestra. Anteroventrally, it has a pocket for receiving the quadrate and quadratojugal.

The vomer forms a vertical thin plate behind the median palatal ridge of the premaxilla and divides the choanae from the middle. Its posterior border with the palatines and pterygoid is unclear.

The palatines flush with surrounding palatal elements. Their rugose anterior pad sutures with the posteromedial process of the premaxilla and separates the maxilla from the border of the choana. Their laminar posterior portion is smooth and forms the medial side of the lateral wall of the choana. The two palatines are separated by the vomer. No ectopterygoid is visible in this specimen.

The pterygoids have the typical ‘X’ -shape as in all dicynodonts. The robust anterior pterygoid rami are elongated and contact the maxilla. Their anterior tips are narrow ventrally as keels (the anterior pterygoid keels), and the ventral ridge on the posterior portion is indistinct and merges into the smooth median pterygoid plate. The median pterygoid plate is transversely wide, with a low crista oesophagea on the ventral surface. The oblate interpterygoid vacuity is short but wide and opens anteroventrally. The quadrate rami are thin, ribbon-like structures without twists and are directed more laterally than posteriorly (the two rami forming an angle of ~120°).

The right epipterygoid is preserved. It is like a curved strap resting on top of the pterygoid. Its footplate extends from the quadrate rami to the lateral side of the medial plate, the ascending process contacts the parietal, and the short anterior process is partially preserved above the pterygoid [Figure 2C: see original paper].

The parabasisphenoid expands posteriorly and forms two lateral ridges. Medial to the ridges lie the paired, ventrally-directed openings of the internal carotid canals. The posterior portion of the bone turns ventrally and forms the anterior surface of the basal tubera. The parabasisphenoid bears an elongate cultriform process anteriorly, which is damaged but visible through the interpterygoid vacuity in ventral view.

The basioccipital forms the major portion of the basal tubera, which is strongly rounded with anterior and posterior tips curving toward each other and nearly enclosing the fenestra ovalis. The basal tuber is inflated and extends ventrally far beyond the palate. The intertuberal region is smooth, U-shaped, and lacks an intertuberal ridge.

Two strips on the dorsal margin of the occiput are identified as the relict of the tabular by Cheng (1980). They do not extend onto the dorsal surface of the intertemporal bar and cannot be observed in dorsal view. The postparietal is mainly exposed on the occiput, although it also has a small exposure on the intertemporal skull roof. It curves posterolaterally and forms a concave area on the top of the occiput [Figure 2D: see original paper]. Its ventral and lateral borders are unclear, but it appears to be separated from the squamosal by the tabular.

Below the postparietal, the supraoccipital forms the dorsal margin of the foramen magnum. No distinct suture is observed between the supraoccipital, exoccipitals, opisthotics, and basioccipital, with these elements fused as a single periotic element as in many dicynodonts (Kammerer et al., 2019; Liu, 2021). The foramen magnum is small and nearly square, lying ventrally on the occiput. Lateral to the foramen magnum and above the occipital condyle lie two knob-like processes for articulation with the proatlases. The small occipital condyle is subspherical in posterior view, with a circular central depression. The ovoid jugular foramen, lateral to the occipital condyle, is the passage for the glossopharyngeal (IX), vagus (X), and spinal accessory (XI) nerves as well as the internal jugular vein.

The paroccipital process is almost laterally directed. Its lateral edge, which sutures to the squamosal, draws into a posteriorly-directed process for the dorsal portion, similar to the tympanic process of *Dicynodontoides* (Cox, 1959). On its dorsolateral surface, a depression accommodates the posterolaterally directed posttemporal fenestra. The small posttemporal fenestra lies at the level of the top of the foramen magnum.

IVPP V 11674. The skull is nearly complete, except that the left caniniform process and tusk, pterygoids, and parabasisphenoid are incomplete, and the stapes and quadrates are missing. It is the best-preserved skull among available specimens, slightly shorter than the holotype, with an occiput not as expanded as in the holotype [Figure 3: see original paper] and occipital width less than the dorsal length of the skull (Supplementary file 1).

The caniniform process lies slightly ventral to the anterior extended line of the zygomatic arch, with the tusk on the medial margin of the caniniform process. The tusk is longer and more robust than in the holotype, with an exposed right tusk length of 65 mm. The tusk base has an elliptic cross-section measuring 24 mm at its greatest diameter. Wear facets lie on both the anterolateral and medial sides, with the anterolateral facet smaller but deeper. Striations are clearer and denser near the tip, mainly arranged along the long axis of the tusk. The right tusk shows four distinct layers, possibly related to its age.

The snout tip is sharper than in the holotype [FIGURE:2, 3]. The premaxillae have sword tip-like posterodorsal processes. The frontal has an anteromedial process that approaches the premaxilla. The narrow intertemporal bar forms a 135° angle with the frontal in lateral view [Figure 4: see original paper].

A midline parietal ridge lies posterior to the pineal foramen. Although the quadrate is lost, the dorsal process of the right quadratojugal still rests in the fossa of the squamosal.

The lacrimal does not extend anteriorly as far as in the holotype. The prefrontal has distinct ridges and furrows on the lateral surface. The zygomatic arch is nearly flat dorsoventrally for the orbital portion [Figure 4A: see original paper].

Posterior to the palatine pad, the elongate lateral palatal foramen lies between the palatine and anterior ramus of the pterygoid. The ectopterygoid has a clear suture with the pterygoid and extends anteriorly beyond the anterior pterygoid ramus. This bone is fused to the pterygoid in the holotype, possibly representing a later ontogenetic stage. The labial fossa is bordered by the maxilla laterally and palatine medially, while the jugal contributes only a small portion of its posterior border. The interpterygoid vacuity is short but wide and opens anteroventrally. The pterygoid quadrate processes are missing. The parabasisphenoid is strongly curved ventrally, and the basal tubera is inflated.

The dorsal margin of the occiput extends only slightly dorsal to the squamosals [Figure 4B: see original paper] and is less developed than in the holotype. It is unclear if the tabular is present. The upper margin of the supraoccipital can be demarcated by a bulge of bone forming a pair of 'wings'.

Lower jaw. The lower jaw is almost complete except for the anterior margin of the dentary symphysis [Figure 5: see original paper]. It is short (18 cm), only about half the skull length.

The dentary symphysis is anteroposteriorly short but dorsoventrally tall and nearly square-shaped in dorsal view. The symphysis is thickened anteroventrally. There is no distinct ridge on the edge between the anterior and lateral dentary surfaces. The anterior and lateral surfaces of the dentary symphysis are rugose, while the dentary lateral surface is smooth above the mandibular fenestra. The dentary dorsal margin forms two sharp ridges, of which the medial one is taller and forms a dorsally-convex blade [Figure 5B: see original paper]. On the dentary table, the area between the two ridges is slightly concave, posteriorly developing into a distinct posterior dentary sulcus.

Posteriorly, the dentary sends two rami: the longer dorsal one forms the dorsal margin of the mandibular fenestra and contacts the surangular, while the ventral one is a triangular process lateral to the angular. The lateral dentary shelf increases in height anteriorly from a small ridge above the mandibular fenestra.

The splenial is fused in the symphysis, with its anterior process exposed in ventral view. Along the midline are two fossae: a shallow one between the dentary and splenial, and a deep one within the splenial. The splenial has no lateral exposure. It partially covers the angular medially and is covered by the prearticular laterally.

The angular is the second largest bone in the lower jaw. Anterolaterally, it has a trough for receiving the posterior process of the dentary. In lateral view, it bifurcates into two rami by the trough: the short anterodorsal ramus is triangular, extending to the anterior margin of the mandibular fenestra, and the long anteroventral ramus inserts between the dentary and splenial and contributes to the symphysis. Posteriorly, the angular bears a large, rounded reflected lamina that is widely separated from the articular. Ventral to the lamina is a small posteroventrally-directed process that should be part of the reflected lamina but is separated from the main body by a deep notch. Medial to the reflected lamina, the angular contacts the articular posteriorly and the surangular posterodorsally, and is covered by the prearticular medially.

The surangular lies between the dentary and articular, partially covered by the prearticular medially. The prearticular is a long strip-like bone that completely covers the mandibular fenestra medially. Posteriorly it is partially fused to the articular. The articular has a short anterior process extending between the prearticular and surangular. The lateral condyle is much wider than the medial one, with a well-developed retroarticular process that curves forward.

IVPP V 6033. The dorsal portion of the skull was eroded, with only the palate and occiput preserved with the lower jaw [Figure 6: see original paper]. It is similar to IGCAGS V315 in size but has a less inclined occiput, giving it the greatest basal length (31 cm). Its occiput has a height slightly greater than half the width as in IGCAGS V315, but the skull maximum length is smaller than the latter.

The caniniform process is incomplete but similar to previous specimens. The tusk is similar in size to that of IVPP V 11674, but the distance between the two tusks (9 cm) is wider. The zygomatic arch has flat dorsal and ventral surfaces. The two sides are less convergent than in previous specimens, forming an angle of ~35° (compared to >45° in IGCAGS V315 and IVPP V 11674). The temporal fenestra also has a length greater than width.

On the palate, the interpterygoid vacuity is relatively small and lies dorsal to the anterior margin of the medial pterygoid palate. The parabasisphenoid is strongly curved ventrally and attached to the anterior side of the basal tuber. No tabular can be identified on the occiput. The occipital condyle is larger than that of IGCAGS V315, and the fenestra magnum appears wider as well.

The lower jaw is nearly complete but occluded with the skull, with a length of 20 cm, about half the skull' s dorsal length. It is similar in shape to the lower jaw of V 11674. The reflected lamina of the left angular diverges laterally near the middle of the lower jaw, and the ventral portion of the angular was eroded.

This specimen was compared with the holotype of *S. xilougouensis*, and the following differences were proposed (Li, 1980): narrower skull with occipital width around 3/4 skull length; snout tip obtuse and wider; larger occipital condyle and foramen magnum; poorly developed caniniform process; longer and stouter tusks that are more widely spaced; zygomatic arch nearly flat dorsoventrally.

IVPP V 11677. This specimen is preserved like IVPP V 6033: the dorsal surface was eroded, and the lower jaw is occluded with the skull [Figure 7: see original paper]. It is slightly smaller than V 6033 and has the largest known tusks, spaced 10 cm apart at the roots. The right tusk bears a wear facet on the anterolateral side that is 40 mm in length, with dense striations in the axial direction near the tip. It also bears a less distinct facet on the medial side. The caniniform process is robust to contain the large tusk, with a curved medial border of the rough area, not straight as in the holotype. The labial fossa is quite large.

The zygomatic arch below the orbit is rod-like. The two sides also form a small angle as in V 6033 and are less convergent than in IGCAGS V315 and V 11674. The maxillary zygomatic process extends posteriorly to the level of the anterior margin of the postorbital, slightly further than in other specimens.

The median pterygoid plate has a low and wide crista oesophagea. The two quadrate rami are slender, forming an angle of ~120°. Their tip inserts into the quadrate, stapes, and paroccipital process of the periotic. The interpterygoid vacuity is sub-triangular and opens ventrally. Its anterior margin lies anterior to the medial pterygoid plate. The parabasisphenoid runs dorsally across it and divides it into two openings. The parabasisphenoid is slightly curved ventrally, but not as strongly as in previous specimens. The epipterygoid is preserved in the dorsal process on the right side.

The quadratojugal is fused to the dorsal surface of the quadrate lateral condyle, with the two bones forming a quadrate-quadratojugal complex. The quadratojugal dorsal process is fan-like within the shallow squamosal lateral pocket, with its dorsal margin loosely connecting with the squamosal. The quadrate dorsal process is smaller than that of the quadratojugal. The right quadrate condyles are exposed in ventral view because the articulated lower jaw slid upwards [Figure 7A: see original paper]. The lateral surface of the median condyle is attached by the stapes on the ventral flange and by the pterygoid quadrate process and paroccipital process on the dorsal concave area.

Both stapes are preserved in situ. It is a column-like bone with a constricted waist. Its medial surface articulates with the fenestra ovalis, and the larger lateral surface articulates with the quadrate. The occiput is quite wide with a rectangular shape [Figure 7D: see original paper]. The occipital condyle is relatively large, and the foramen magnum has a width subequal to its height.

The lower jaw is estimated to be 20 cm in length including the missing dentary tip. The symphysis is robust and high, with a length of 7 cm. A middle ridge develops on the dentary anterior surface, widening and decreasing in height ventrally. The reflected lamina of the angular is incomplete on either side but preserves a ventrally directed portion, though it is unknown if it is a separate process as in V 11674.

IVPP V 11675. The dorsal portion of the skull is almost fully eroded except for bone around the pineal foramen [Figure 8: see original paper]. The right lateral side and palate are relatively complete. The skull has a width of ~36 cm and basal length of ~27 cm. The tusk is short but bulky, with a diameter of 26 mm and exposed length of 55 mm. The caniniform process is rounded, with the tusk on its medial side, lying slightly below the anterior extension line of the zygomatic arch.

The right zygomatic arch is complete, with its orbital portion rod-like. The two zygomatic arches form a large angle (59°). The maxilla extends posteriorly to the level of the anterior margin of the postorbital. The squamosal extends anteriorly beyond half of the orbital ventral length. The oval pineal foramen is quite large [Figure 8D: see original paper]. The lingulate preparietal lies in the concave area anterior to the pineal foramen and forms the anterior wall of the latter. The preserved intertemporal bar is the same as in other specimens.

The interpterygoid vacuity lies far anterior to the median pterygoid plate and is longer than wide. Its dorsal openings are small [Figure 9: see original paper]. The crista oesophagea is a low ridge on the median pterygoid plate. The parabasisphenoid is nearly flat, with only the two posterolateral corners curving to an angle of ~30° and forming a small portion of the basal tubers. The openings for the internal carotid canal are not clear on the ventral surface, but the dorsal openings sit deeply within a triangular pyramid-shaped sella turcica that houses the pituitary gland. The sella turcica is formed only by the parasphenoid.

The right squamosal is nearly complete. The occiput is relatively low, with occipital height about half its reconstructed width. The occiput is strongly inclined posteriorly. The occipital condyle is semicircular with a concave dorsal surface. The right quadrate-quadratojugal complex is preserved in the anteroventral pockets of the squamosal, with the fan-like dorsal process of the quadratojugal firmly sutured with the squamosal [Figure 8C: see original paper].

The absolute size of the lower jaw is larger than that of V 11674. The robust symphysis is occluded with the snout [Figure 8B: see original paper]. The vertical portion of the reflected lamina is present, but it is unknown if it is a separate process [FIGURE:8E, F].

IVPP V 17904. The skull was sheared and skews to the right side [Figure 10: see original paper]. The posterior portion including the occiput is not preserved. This skull is smaller than V 11674, with an estimated basal length of 21 cm. The caniniform process is only weakly developed. The tusk is short and thin. The zygomatic arch curves laterally, and the orbit can be partially observed dorsally, similar to V 11674.

The labial fossa is small and rounded, with most of the posterior margin formed by the jugal, though the posterolateral side is covered by the maxilla if complete [Figure 10B: see original paper]. The median pterygoid plate has no distinct ridge, but a suture in that position indicates unfused pterygoids. The interpterygoid vacuity is round and opens ventrally. It is almost covered dorsally by the parabasisphenoid, with only a small opening present on the left side.

The parabasisphenoid expands posteriorly and forms two lateral ridges. Medial to the ridges, paired depressions lie on the anterior portion of the parabasisphenoid. Posterior to the shallow depressions, the paired ventrally-directed openings of the internal carotid canals lie on the narrowest part of the parabasisphenoid. The basal tubera are not well developed, and the groove between them is shallow.

IVPP V 11676. The skull measures 16 cm in basal length [Figure 11: see original paper]. It has undergone anteroposterior compression with many cracks. There is no distinct midline ridge on the dorsal surface of the snout. The premaxillae have the same sword tip-shaped posterodorsal processes as in the holotype. The frontal anteromedial processes approach the premaxilla, and the nasals are nearly divided by them. The small prefrontal is nearly semicircular and forms only a small portion of the orbital dorsal margin. The preparietal is almond-like, lying at the level of the postorbital bars. The intertemporal bar is relatively wider compared to larger specimens. The postorbitals form the lateral ridges of the intertemporal bar, bracing a concave area formed by the parietals. A weak protuberance lies along the axial line posterior to the pineal foramen as in V 11674.

The caniniform process is less developed, and the rough area is narrower than in large specimens [Figure 11: see original paper]. The tusks are small and short. The triangular lacrimal bulges laterally and approaches the septomaxilla. The small lacrimal foramen lies within the middle of the orbital anterior wall. The zygomatic arches are convex laterally, so the orbits open somewhat dorsally. The orbital portion is more or less rod-like. The orbit has large exposure in dorsal view. The intertemporal bar is slightly convex dorsally and forms a 130° angle with the frontal in lateral view. The postparietal has a small exposure on the skull roof. Both sides of the quadrate-quadratojugal complex are preserved, though the right one is partially detached from the skull [FIGURE:11E, F].

The palate is poorly preserved with no clear sutures visible [Figure 11C: see original paper]. The labial fossa is small. The skull is broken along the parabasisphenoid as in V 11674. It appears the medial pterygoid plate was pushed upwards compared to the basal tuber by compression.

The occiput is relatively high [Figure 11D: see original paper], with an occipital height to width ratio of 0.79, slightly smaller than that of the holotype (0.82) and V 11674 (0.84), but much greater than in V 6033 (0.62) and V 11677 (0.65). The foramen magnum is rounded. The posttemporal fenestra is small. The occipital condyle is damaged but should be tri-radiate in posterior view.

The basic pattern of the lower jaw is the same as in V 11674 [Figure 12: see original paper]. The symphysis is complete in this specimen, with its dorsal margin distinctly curved dorsally, higher than the dentary rami. A low midline ridge is present on the anterior surface of the symphysis and disappears at half the height. On the dorsal margin of the dentary, the medial edge forms a dorsally-convex cutting blade [Figure 12C: see original paper]. Although the reflected lamina is incomplete, a remnant of the vertical ventral portion on the right side is clearly separated from the upper portion [Figure 12B: see original paper], indicating this portion could be the same as that of V 11674. The reflected lamina is far from the articular.

IVPP V 30725. The skull is heavily eroded, with only two caniniform processes, zygomatic arches, posterior portion of the skull roof, and middle portion of the palate preserved, while the lower jaw is almost complete [Figure 13: see original paper]. The skull dorsal length is estimated as ~18 cm. The flat caniniform process wraps the lateral side of the tusk. The maxilla extends posteriorly only to the middle of the orbit. The orbital portion of the zygomatic arch is dorsoventrally flat. The interpterygoid vacuity is round and opens ventrally. The quadrate rami form an angle of 115°. The lower jaw is 11 cm in length. The reflected lamina is incomplete.

IVPP V 30729. Most of the dorsal and right lateral side of the skull is preserved [Figure 14: see original paper]. The preserved skull length is 10 cm, with an estimated dorsal length of 12 cm. This specimen is the smallest among known specimens and is likely a juvenile.

The premaxillae are unfused. They have slender posterodorsal processes, and the posterolateral margins are formed by one straight line rather than two segments as in other specimens. The maxilla has a poorly developed and broken caniniform process that lies slightly below the anterior extended line of the zygomatic arch. The frontal anteromedial processes form a sharp angle and nearly touch the premaxillae. The prefrontal is relatively small, while the lacrimal is a large element forming the anterior orbital wall. The small lacrimal foramen lies in the middle of the anterior orbital wall. The lacrimal sends a triangular process to cover the jugal dorsally. The maxilla sends a long posterior process that contacts the squamosal laterally, with its posterior end inserting between the squamosal and jugal on the ventral surface of the zygomatic arch and extending to the level of the anteroventral margin of the postorbital.

IVPP V 30726. Only the palate of the skull is preserved and exposed in dorsal view [Figure 15A: see original paper]. The lower jaw is articulated to the skull. The two quadrate rami form an angle of 120°. The exposed braincase has a rounded fossa formed by the parabasisphenoid anteriorly, exoccipitals posteriorly, and prootic and opisthotic laterally. The sutures are still identifiable, indicating a young stage. It appears only the left ramus of the lower jaw is preserved and partially exposed in dorsal view. Identification of this specimen is mainly based on postcranial bones.

5.2 Postcranial Skeleton

Postcranial elements of *Shaanbeikannemeyeria* are preserved in IVPP V 6033, V 11676, V 30726, and possibly V 30728. The postcranial skeleton is nearly complete in V 30726, but the bones are not in good condition and preparation is incomplete. Description of vertebrae and ribs is based on V 30726.

Axial skeleton. Most cervical vertebrae are not exposed except for neural spines of the last few, but their number can be counted based on articulating ribs [Figure 15B: see original paper]. The first preserved rib is a very short one (<2 cm) close to the head, likely belonging to the axis. The following ribs have a wide head with identifiable capitulum and tuberculum, though no distinct groove separates them. The 7th rib is similar to the 6th in shape but is identified as the first dorsal based on its position, as the first dorsal is similar to the last cervical in many dicynodonts (Sun, 1963; Bandyopadhyay, 1988; Liu, 2021). The dorsal number is counted as 15 [Figure 15: see original paper]. The sacral region is not well preserved, but the number should be no less than 5 based on ilium and vertebra length. The tail is short with ~8 caudal vertebrae. This specimen has the lowest number of dorsal and presacral vertebrae among all dicynodonts with known counts (Liu, 2021).

The sternum is only observed in IVPP V 6033 [FIGURE:16A, B]. It is well ossified but only a small portion is preserved, tentatively identified as the anterior-left portion. There is a mid-keel on the ventral surface and a wide ridge on the dorsal surface.

Pectoral girdles. The scapulae are preserved in IVPP V 6033, V 11676, and V 30726 [Figure 16: see original paper]. It is a narrow, gently arched bone with a dorsally expanding blade. On the anterior margin, below the upper edge of the blade, a sharp ridge runs downwards to the acromion, transitioning from more laterally directed to more anteriorly directed. The ventral margin of the acromion is directed slightly ventrally. A depression lies between the ridge and the blade. In the right scapula of V 11676, the scapular ventral margin is smoothly convex and the lateral surface is smooth, though this could be deformation based on the left scapula. The ventral portion below the acromion should be much thinner than the glenoid as in V 6033 [FIGURE:16E, F]. A groove separates the anterior portion from the posterior portion (with glenoid) on the medial side, and a shallow notch presents on the ventral side of the groove, similar to *Wadiasaurus* (Bandyopadhyay, 1988) and less developed than *Turfanodon* (Liu, 2021).

Both clavicles are preserved in V 6033 and V 11676 [Figure 16: see original paper], but only the right clavicle of V 6033 is nearly complete and described here. The dorsal portion is slightly wider than the ventral portion. The dorsal end is wide, while the medial end has a triangular shape, quite different from those in *Sinokannemeyeria*, which has a sharp dorsal process and narrow medial end (Sun, 1963). The articular groove with the interclavicle is indistinct. The dorsal portion is incomplete, and the medial (ventral) end is more obtuse in V 11676.

The incomplete interclavicle is attached to the dorsal surface of the right clavicle in V 11676 [FIGURE:16I, J]. A boss is developed along the midline, and the dorsal surface is smoothly concave.

Forelimb. The humerus, ulna, and radius are preserved in IVPP V 6033 and

V 30726, while only humeri are preserved in V 11676 [FIGURE:15-17].

The humerus is nearly flat, even accounting for the incomplete deltopectoral crest in IVPP V 6033 [Figure 17: see original paper]. However, this should be artifactual because the distal end is twisted relative to the proximal end in small specimens. The articular surface on the proximal head is convex and slightly expanded dorsally. The proximal end for insertion of M. subcoracoscapularis is poorly preserved but is a rounded, rugose area. Distally, there is a dorsoventrally flattened area for insertion of M. latissimus dorsi. More distally, the entepicondylar foramen lies at mid-shaft. The deltopectoral crest has a thick, rough (ventral) edge forming an obtuse angle with the distal edge. The ectepicondyle is wider than the entepicondyle. The supinator process is undeveloped in IVPP V 11676 and V 30726 but present in V 6033 [FIGURE:15, 16]. The articular surface on the distal end has little exposure on the dorsal surface.

The ulna is a robust bone with an anteroposteriorly compressed shaft [Figure 17: see original paper]. There is no evidence for the olecranon process as a separate ossification. The olecranon process is low and rounded, similar to *Kannemeyeria simocephalus* (Govender, 2005), but quite different from that of *Sinokannemeyeria* and *Wadiasaurus* (Sun, 1963; Bandyopadhyay, 1988). The sigmoid notch is gently concave with a slightly elongated surface. Below the sigmoid notch is a facet for reception of the lateral extension of the radius, observed only on the right ulnae of V 6033 and covered by the radius on the left side of V 30726.

The radius is shorter than the ulna [Figure 17: see original paper]. It has a slender shaft and expanded ends. The proximal end is a shallow concave surface surrounded by a prominent rim. Below the proximal end, a rugose surface presents on the posterolateral side, part of it forming the facet on the proximal end of the ulna. The anterior surface is flat, while the posterior surface is convex and bears a ridge running proximodistally. The distal end is an oval concave surface for articulation with the radiale.

Pelvic girdle. All pelvic bones are preserved in IVPP V 30726 [Figure 15D: see original paper]. The ilia are exposed in lateral view, with left pubis and ischium mainly in lateral view and right pubis and ischium in medial view.

The ilium has a flat, thin, dorsomedially oriented plate (iliac blade). The iliac anterior process is much longer than the posterior process, which is short and tapers almost to a point. The blade constricts to a neck as wide as the acetabulum. Ventrally, the bone thickens and expands, bearing the acetabular facet laterally and facets for the pubis anteroventrally and ischium posteroventrally. The medial surface is not exposed but should bear facets for at least five sacral ribs.

The pubis is a thick but short bone, fused to the ischium as one plate on the right side but separated on the left. It has a concave lateral surface. The anterior edge is poorly known, but its unfinished rough end—the area for the cartilaginous epipubis—is exposed. The posterior margin is notched in the middle for the obturator foramen.

The ischium is broad with a convex outer surface and concave inner surface. Below the acetabular part, the anterior margin is deeply notched for the obturator foramen, below which this margin meets the pubis. The bone is thickened posteriorly and forms a posterodorsal flange.

Hind limb. The right hind limb is nearly complete in IVPP V 30726 [Figure 15: see original paper], while femur, tibia, and fibula are preserved in V 6033 [Figure 17: see original paper].

Both femora of V 30726 are articulated to the acetabulum and almost exposed in dorsal view [Figure 15: see original paper]. The left femur of V 6033 is nearly complete, with a length of 25 cm [FIGURE:17J, K]. The proximal expansion is as wide as the distal. The head is a moderate swelling on the dorsal margin, not particularly rounded but slightly encroaching on the anterior surface. The trochanter major has a rugose surface and is slightly convex outward. This area has many striae but is smoother in the young specimen (V 30726). The insertion of M. iliofemoralis is a distinct crest on the lateral surface. The intertrochanteric fossa is shallow. The shaft is flattened with a minimum width of 5 cm. Distally, the articulating condyles are well developed, with the posterior condyle larger and more rounded. The ventral articulating surfaces of the condyles are nearly at the same level. The popliteal fossa is shallow and wide.

The fibula is slender and bows laterally somewhat away from the tibia [Figure 15E: see original paper]. It also bows anteriorly, with slightly expanded ends.

The tibia is a robust bone expanded proximally to form articular facets for two femoral condyles, which are concave and separated by a prominent crest [FIGURE:15E, 17N–Q]. The proximal side of the bone is expanded anterolaterally as the cnemial crest, which narrows ventrally and disappears before reaching half the length. A wide groove lies between the cnemial crest and lateral margin. The shaft becomes narrow in the middle. The medial/posterior margin of the bone is strongly concave, while the lateral/anterior margin is nearly straight. The distal end is less expanded than the proximal, and the distal articular facet is oval, slightly concave in the lateral half and convex in the medial.

The right pes was rotated relative to the tibia and fibula [Figure 15E: see original paper]. Most elements are preserved and mainly exposed in ventral view, while digit V is in lateral view; only three phalanges of digits IV and V are lost [Figure 15F: see original paper].

The astragalus and calcaneum are articulated, with the former partially covering the latter in dorsal view [Figure 15E: see original paper]. The two bones are similar in size, but the astragalus is nearly square and much thicker. The proximal articular facet for the tibia is convex. A distinct sulcus runs from the proximal corner to the lateral margin on the ventral surface toward the calcaneum. The calcaneum is a rounded plate thin in the middle but with thickened margins, especially the medial margin. A shallow depression presents in the middle on both dorsal and ventral surfaces. A shallow notch on the medial margin of the ventral surface connects to the astragalus sulcus. Three distal tarsals are ossified and ellipsoid in shape. Distal tarsal 3 is the largest, while distal tarsal 2 is the smallest. Distal tarsal 3 articulates with metatarsals 3, 4, and 5.

The metatarsals are broad, short, and constricted in the middle. The articulating surfaces on the two sides are transversely elongated. They vary in length: metatarsals 3 and 4 are longest, while metatarsal 1 is shortest but broadest.

The preserved digital formula is 2-3-3-1-2, fitting the general dicynodont digital formula. Except for the ungual ones, the phalanges are quite broad and short, shorter than their respective metatarsals. The last ungual phalanx turns back and ventral to the penultimate phalanx in digits I to III. The ungual phalanges are spatulate and end in rounded tips.

Kannemeyeriiformes ?Parakannemeyeria Sun, 1960

Referred specimen: IVPP V 30727 and V 30730, two partial postcranial skeletons.

Comments: The postcranial bones of V 30730 are slightly larger than corresponding bones in V 30726 and V 11676. Although associated with a juvenile skull (V 30729), the skull size is too small when compared with V 11676 and V 30726, so they should belong to different individuals.

Description. IVPP V 30730 comprises 10 vertebrae, some ribs, left ilium, femur, tibia, and fibula [FIGURE:18A–D]. V 30727 includes some dorsal vertebrae and ribs, paired pectoral girdles, humeri, right ulna, and right radius [FIGURE:18E–N].

In IVPP V 30727, eight dorsal centra are exposed and more than six ribs are preserved. In V 30730, the last six dorsal and first four sacral vertebrae are preserved [FIGURE:18B, D]. The dorsal centra are roughly 2 cm in length in both specimens, indicating they are similar in size. In V 30730, the short ribs are fused to the neural arches. The vertebrae are compressed, so the ribs nearly lie in a plane with the poorly preserved neural spines. Three right sacral ribs are present. The distal end of the first is extremely expanded, with its width (28 mm) much greater than the length of the sacral vertebra (21 mm).

The preserved pectoral girdle elements include right scapula, coracoid, and procoracoid [FIGURE:18E, F]. The scapula measures 17 cm in height, taller than that of V 11675. The posterior side is incomplete, but the preserved portion is similar to that of V 6033 [Figure 16: see original paper]. The coracoid plate is composed of coracoid and procoracoid sutured together. The glenoid is mainly formed by the scapula and coracoid, but the posterodorsal margin of the procoracoid also contributes a small portion. The coracoid foramen lies entirely within the procoracoid close to the posterodorsal corner of the bone. On its medial surface, the coracoid foramen opens dorsally as a groove continuous with the scapular groove. The procoracoid is broken for most of its free margin, while the ventral margin of the coracoid plate is smoothly convex. The coracoid has a long posteroventral process, more similar to *Parakannemeyeria youngi* (IVPP V 972) than *Sinokannemeyeria* (Young, 1937; Sun, 1963).

The right humerus is relatively complete except for the deltopectoral crest [FIGURE:18G, H]. This bone is longer than those of IVPP V 11676 and V 30726, but thinner and more slender, with the shaft also narrower (24 mm at its narrowest place in dorsal view) than described above. The two extremities are poorly ossified, indicating a young stage. The deltopectoral crest forms a large angle with the head, indicating no distinct deformation. A bone identified as the right radius here [FIGURE:18I–K] has a concave area close to the proximal end, which should not be present and is explained as the result of poor ossification of the extremities and deformation during preservation. The right ulna has a poorly ossified proximal end and has lost the distal end [FIGURE:18L, M]. The articular facet for the humerus is poorly developed.

The left ilium preserves the anterior process of the blade and the ventral portion for articulation with the ischium, pubis, and femur [Figure 18A: see original paper]. The iliac facet of the acetabulum faces ventrally for the most part, its lateral rim projects laterally, and the anterior and posterior rims form a sharp angle. The femur, tibia, and fibula are incomplete, both losing proximal and distal ends. They are longer but more slender than corresponding bones of IVPP V 30726.

Discussion. Four kannemeyeriid genera are known in China: *Sinokannemeyeria*, *Parakannemeyeria*, and *Shaanbeikannemeyeria* from North China, and *Xiyukannemeyeria* from Xinjiang (Li and Liu, 2015). The coracoid shows differences from *Sinokannemeyeria*. The humerus is more slender than the similarly sized humerus of *Xiyukannemeyeria* (Sun, 1978). All limb bones are longer but more slender than corresponding bones in IVPP V 11676 and V 30726. These bones are poorly ossified at their extremities, indicating a young age. All known features of these specimens are consistent with *Parakannemeyeria youngi* (Sun, 1963), and this genus was also reported from the lower Ermaying Formation (Cheng, 1980), so they are tentatively referred to *Parakannemeyeria*.

6 Phylogenetic Analysis of Shaanbeikannemeyeria

To test the phylogenetic position of *Shaanbeikannemeyeria*, it was recoded based on available specimens for the revised character list following Angielczyk et al. (2021), Kammerer and Ordoñez (2021), and Liu (2021) (Supplementary file 2). *Turfanodon jiufengensis* and *Kunpania scopulusa* were also coded and added to the matrix. The final dataset consists of 119 operational taxonomic units (OTUs) and 199 characters (23 continuous and 176 discrete-state) (Supplementary file 3). Continuous characters were treated as additive, and eight discrete-state characters were treated as ordered (characters 56, 81, 84, 102, 163, 173, 189, and 199). Data were analyzed using parsimony in TNT v1.5 (Goloboff and

Catalano, 2016), resulting in one most parsimonious tree of length 1267.069.

The tree is mostly identical to that of Kammerer and Ordonez (2021) except for interrelationships within clade A (Kannemeyeriidae), L (*Lystrosaurus*), and P (Placeriinae) [Figure 19: see original paper]. In recent analyses, Kannemeyeriiformes includes non-monophyletic shansiodontids plus two major clades: the Kannemeyeriidae and another clade (B) including the Stahleckeriidae as a subclade (Angielczyk et al., 2017; Kammerer et al., 2019; Kammerer and Ordoñez, 2021; Liu, 2021) [Figure 19: see original paper]. Although members of Kannemeyeriidae are stable, interrelationships among taxa vary considerably. For example, *Kannemeyeria* as a monophyletic genus was recovered by Kammerer & Ordoñez (2021); *Shaanbeikannemeyeria* is an early-divergent taxon (Angielczyk et al., 2017; Kammerer et al., 2019), or forms the sister taxon of *Rechnisaurus* plus *Uralokannemeyeria*.

7.1 Diagnostic Features of Shaanbeikannemeyeria xilougouensis

The premaxillary posterodorsal processes are sword tip-like in *Shaanbeikannemeyeria*, different from the nearly triangular ones in most Triassic kannemeyeriiforms such as *Vinceria* (Bonaparte, 1969; Domnanovich and Marsicano, 2012), *Shansiodon* (Cheng, 1980), *Tetragonias* (Cruickshank, 1967), *Rhinodicynodon* (Kalandadze, 1970), *Acratophorus* (Kammerer and Ordoñez, 2021), *Sinokannemeyeria* (Sun, 1963), *Parakannemeyeria* (Sun, 1960; Sun, 1963), *Xiyukannemeyeria* (Liu and Li, 2003), *Rhadiodromus* (Surkov, 2003), *Rechnisaurus* (Bandyopadhyay, 1989), *Wadiasaurus* (Bandyopadhyay, 1988), *Kannemeyeria* (Renaut and Hancox, 2001), *Dolichuranus* (Damiani et al., 2007), *Rabidosaurus* (Kalandadze, 1970), *Ufudocyclops* (Kammerer et al., 2019), *Dinodontosaurus* (von Huene, 1935; Cox, 1968; Morato, 2006), *Stahleckeria* (Maisch, 2001; Vega-Dias et al., 2005); and from quite narrow processes in *Ischigualastia* (Kammerer and Ordoñez, 2021). This process is absent in *Jachaleria* (Araújo and Gonzaga, 1980; Vega-Dias and Schultz, 2004), uncertain in *Angonisaurus* (Cox and Li, 1983), *Sangusaurus* (Angielczyk et al., 2017; Kammerer and Ordoñez, 2021), *Uralokannemeyeria* (Danilov, 1971), *Moghreberia* (Dutuit, 1988), and unknown in *Eubrachiosaurus* (Williston, 1904; Kammerer et al., 2013), *Zambiasaurus* (Cox, 1969), and *Pentasaurus* (Kammerer, 2018).

The dentary of *Shaanbeikannemeyeria* has a tall, dorsally-convex cutting blade on the medial edge of the dorsal surface (Character 149). This state is only present in some Permian dicynodonts such as *Diictodon* (Sullivan and Reisz, 2005) and *Robertia* (King, 1981), but is unreported in Triassic dicynodonts.

The reflected lamina of the angular of *Shaanbeikannemeyeria* is generally similar to that of *Acratophorus argentinensis* or *Kannemeyeria simocephalus*: large, rounded, and with a concave lateral surface on the ventral portion (Renaut and Hancox, 2001; Kammerer and Ordoñez, 2021). It differs from that of *Sinokan-*

nemeyeria or *Parakannemeyeria*, in which it is elongated with a convex ventral surface (Sun, 1963). However, the ventral portion is separated as a small posteroventrally-directed process in this taxon.

Shaanbeikannemeyeria shares the following features with *Kannemeyeria*, *Rechnisaurus*, and *Uralokannemeyeria*: posterior pterygoid rami forming a large angle (>98°) (C9), palatal surface of premaxilla exposed in lateral view (C44), and median snout ridge present on premaxilla and nasal (C199). The angle formed by the two posterior pterygoid rami (~115°) is largest in *Shaanbeikannemeyeria* (Supplementary file 4).

Shaanbeikannemeyeria shares the following features with *Rechnisaurus* and *Uralokannemeyeria*: preorbital region nearly more than half the basal length of the skull (C1), occiput inclined relative to palate resulting in short skull basal length (C13), snout anterior tip squared off (C35), parietals exposed in midline groove or channel (C72), caniniform process lying slightly below the anterior extended line of the zygomatic arch and dorsal edge of erupted canine tusk anterior to anterior naris margin (C55), with wide lateral extension exposed in dorsal view, and ventral surface of median pterygoid plate with thin median ridge (C115, unknown in *Rechnisaurus*).

However, the occiput is strongly inclined in *Shaanbeikannemeyeria*, giving it the shortest basal length relative to dorsal length among all known kannemeyeriiforms. *Shaanbeikannemeyeria* also has the longest preorbital region relative to skull basal length, though this may be related to its short skull basal length. It differs from *Uralokannemeyeria* and *Rechnisaurus* by the postorbital not extending the entire length of the intertemporal bar and by the oblique ridge on the lateral side of the zygomatic arch in adults.

Shaanbeikannemeyeria is easily distinguished from other Triassic kannemeyeriiforms from North China (*Shansiodon*, *Sinokannemeyeria*, *Parakannemeyeria*) based on complete cranial material by its strongly inclined occiput. For incomplete specimens, it can also be differentiated by the sword tip-like premaxillary posterodorsal processes, dorsally-convex cutting blade on the medial edge of the dorsal surface of the dentary, and reflected lamina with a separated posteroventral process. It is differentiated from *Shansiodon* by its larger size, relatively small temporal fenestrae, and intertemporal bar that is wide, not crest-like, and raised from the skull roof. It is differentiated from *Sinokannemeyeria* and *Parakannemeyeria* by its short snout, premaxillary lateral surface anterior to external naris without lateral extension, small caniniform process and tusk, narrower interorbital region, and longer intertemporal bar.

7.2 Variations within Shaanbeikannemeyeria

In specimens of *Shaanbeikannemeyeria*, caniniform processes are well developed on all skulls with basal length $ 24*cm*, *whilepoorlydevelopedonallsmallerskulls*.*Specimensareclassifiedintoth*
adults($24 cm), subadults (10 cm < skull basal length < 24 cm), and juveniles (<10 cm).

A distinct feature present in IGCAGS V315, IVPP V 6033, and V 11674 is that the interpterygoid vacuity lies dorsal to the anterior margin of the median pterygoid plate, with anteroposterior length much less than width. In these specimens, the parabasisphenoid is strongly curved and nearly vertical (broken in V 11674). In IVPP V 11675, V 11677, and V 17604, the parabasisphenoid is well-preserved and only slightly curved ventrally. The former condition could result from deformation from compression of the occiput rather than natural state. In the smaller IVPP V 11676, the parabasisphenoid is also broken, possibly due to compression. Thus, the strongly inclined occiput in some specimens (e.g., IGCAGS V315, IVPP V 11674) could be exaggerated by deformation, but *Shaanbeikannemeyeria* still has the most strongly inclined occiput because the undeformed specimen (IVPP V 11677) still has the greatest value for character 13 (Supplementary file 4).

Specimens show many distinct variations in cranial morphology, even among adults (Table 2). The occiput varies in width relative to height, with the holotype having the widest occiput even though its skull length is shorter than other specimens. The caniniform process is undeveloped in pre-adult specimens. Characters have a random distribution among these specimens, making it unlikely that they represent more than one species, as in the classification of Li and Liu (2015). However, different shapes of the caniniform process could result from dimorphism, as shown in some Triassic dicynodont species (Kammerer and Ordoñez, 2021).

Table 2. Variations of some cranial features among different specimens

Specimen	Ratio of occipital width/height	Snout tip	Orbital portion of zygomatic arch	Caniniform process
IGCAGS V315	obtuse	sharp	rod-like	rounded
IVPP V 11674	obtuse	sharp	nearly flat dorsoventrally	rounded
IVPP V 6033	obtuse	sharp	nearly flat dorsoventrally	undeveloped
IVPP V 11675	sharp	sharp	rod-like	rounded
IVPP V 11676	sharp	sharp	rod-like	rounded
IVPP V 11677	sharp	sharp	rod-like	rounded

Specimens of *S. xilougouensis* also display ontogenetic variations. The caniniform process and tusk are undeveloped in pre-adult specimens (IVPP V 11676, V 17904, V 30726), and the dorsal edge of the erupted canine tusk still lies below the naris but anterior to the anterior naris margin in adults. The maxillary posterior process extends only to the middle of the orbit in small specimens (IVPP V 30725, V 30726), but approaches or even extends posterior to the anterior margin of the postorbital bone in large specimens (IVPP V 11674, V 11677). The frontals are close to the premaxilla in pre-adults (IVPP V 30726, V 11676) but widely separated in adults. The intertemporal bar is wide and the parietals are well exposed in V 11676, but becomes a narrow bar with parietals exposed in the midline groove in adults. The ectopterygoid is a distinct bone in smaller specimens but cannot be identified in the holotype. The oblique ridge is absent on the lateral side of the zygomatic arch in subadults (V 11676) but present in adults. The ratio of the deltopectoral crest relative to total humerus length increases through ontogeny (C18, [Figure 19: see original paper]), while relative orbital size, relative temporal fenestra size, width of median pterygoid plate relative to basal skull length, and maximum height of postdentary bones (excluding reflected lamina of angular) relative to height of dentary ramus decrease (C16) (Supplementary file 4).

7.3 Coexistence of Two Kannemeyeriiform Taxa in Lower Ermaying Formation

All studied cranial materials belong to *Shaanbeikannemeyeria*. The skull of IVPP V 30726 is poorly preserved, but available features such as the inclined occiput and pterygoid posterior rami forming a large angle are consistent with known features of *Shaanbeikannemeyeria*, and postcranial elements are nearly identical to those of V 11676 and similar to those of V 6033. IVPP V 30727 and V 30730 represent a different taxon, possibly *Parakannemeyeria*. It should also be noted that two genera possibly coexisted in the *Sinokannemeyeria-Shansisuchus* Assemblage Zone (Liu, 2015).

8 Conclusions

Shaanbeikannemeyeria includes only one valid species, *S. xilougouensis*. It is characterized by an occiput strongly inclined relative to the palate resulting in short skull basal length, sword tip-like premaxillary posterodorsal processes, a tall and dorsally-convex cutting blade on the medial edge of the dorsal surface of the dentary, reflected lamina with a separated posteroventral process, and 15 dorsal vertebrae. *S. xilougouensis* is not a basal member within the Kannemeyeriidae. Another kannemeyeriiform genus, possibly *Parakannemeyeria*, coexisted with *Shaanbeikannemeyeria* in the lower Ermaying Formation.

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