China Geology 6 (2023) 685−694

China Geology

Journal homepage: http://chinageology.cgs.cn
https://www.sciencedirect.com/journal/china-geology

The morphology and histology of a juvenile *Sinokannemeyeria* from the Middle Triassic Ermaying Formation of Shanxi, North China

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ARTICLE INFO

Article history:
Received 17 May 2021
Received in revised form 26 December 2021
Accepted 13 January 2022
Available online 23 March 2023

Keywords:
Tetrapods
Sinokannemeyeria
Histology
Bone microstructure
Middle Triassic
Geological survey engineering

ABSTRACT

Kannemeyeriiformes were dominated tetrapods in the Middle Triassic terrestrial faunae of China. Although abundant materials of *Sinokannemeyeria* have been collected, their postcranial morphology information is not well studied, especially the juveniles. This paper presents a description of an articulated Sinokannemeyeria skeleton from the Middle Triassic Ermaying Formation and reports the histological microstructure of its femur. This specimen represents a late-stage juvenile based on the histological information. For the first time, this specimen offers insights into the postcrania information of juvenile *Sinokannemeyeria*.

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1. Introduction

Therapsids were dominated tetrapods of Permo-Triassic terrestrial ecosystem. Among them, dicynodonts were one of the major tetrapod herbivores (Angielczyk KD and Kammerer CF, 2018). During the Triassic, *Lystrosaurus* survived in the end Permian mass extinction and became the most abundant tetrapods in the Early Triassic (Botha J 2020; Botha J and Smith RMH 2007; Nicolas M et al., 2010; Viglietti PA et al., 2021; Smith R et al., 2012), Kannemeyeriiformes were worldwide distributed in the Middle Triassic (Kammerer CF et al., 2011; Kalandadze NN, 1970; Kalandadze N and Sennikov AG, 1985; Sun AL, 1963; Surkov MV, 2000; Young CC, 1959), especially in North China, and were the dominated herbivorous tetrapods in many terrestrial faunae.

In North China, tetrapod fossils have been reported from the Heshanggou, Ermaying and Tongchuan formations among all Triassic terrestrial deposits (Li JL et al., 2008; Liu J and Fernando A, 2015; Liu J, 2015, Liu J and Sullivan C 2017; Sun AL, 1980; Sun AL et al., 1992). The majority of Triassic tetrapod fossils were discovered in the Ermaying Formation. Its lower section yielded the *Shaanbeikannemeyeria-Fugusuchus* assemblage, while the upper section yielded the *Sinokannemeyeria-Shansisuchus* assemblage (or *Shansidon* assemblage) (Li JL and Cheng ZW, 1995; Liu J, 2015; Sun AL,1980). The latter assemblage, found in the upper part of the Ermaying Formation from Shaanxi, Shanxi and Henan provinces in North China, has been referred to as the "*Sinokannemeyeri* a Fauna" for over half a century (Liu J, 2018; Sun AL, 1963, 1980).

The Triassic deposits within Qinshui Basin of Shanxi are continuous and well-outcropped, primarily composed of sediments from the Ermaying and Tongchuan formations (Liu J, 2015; Xie LJ, 2014, 2016, 2021; Young CC, 1959). Abundant Kannemeyeriiformes fossils have been discovered in Wuxiang, Yushe and Lishi counties in Shanxi Province, resulting in the establishment of three genera: the medium size *Sinokannemeyeria*, *Parakannemeyeria* , and dwarf size *Shansiodon* (Cheng ZW, 1980; Li JL, 2009; Liu, 2015; Liu J

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Literary editor: Li-qiong Jia
doi:10.31035/cg2023030
2096-5192/© 2023 China Geology Editorial Office.

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et al., 2001; Liu J and Fernando A, 2015; Sun AL, 1960, 1963; Xie LJ, 2014, 2016, 2021; Yeh HK, 1959; Young CC, 1937, 1957, 1961; Young CC et al., 1959). Subsequently, fossils from Sangbi (Wu XC et al., 2001) and Baidaoyu (Liu J, 2015) of Shanxi Province showed that the archosaurs and "kannemeyeriids" were both extended into Member I of the Tongchuan Formation, their presence increases the content and time extension of the *Sinokannemeyeria-Shansisuchus* Assemblage. However, the boundaries, definition and biostratigraphic designation of this assemblage remained open to revision (Liu J, 2015).

Fossil juveniles of Kannemeyeriiformes are relatively rare among previously discovered Chinese materials. Cheng ZW (1980) established *Sinokannemeyeria sanchuangheensis* based on a 15 cm long skull with discernible sutures between all elements, suggesting that it could be a juvenile. Some bones were referred to the juvenile of *Parakennmeyeria youngi* (Sun AL 1963), but the skull is about 36 cm in length and too big to be a juvenile. Here the authors report an articulated specimen from the Ermaying Formation of Yushe County, Shanxi Province, China. Based on morphological analysis, it is identified as *Sinokannemeyeria* and provides additional postcranial characteristics of this species.

The growth records of individuals are deeply preserved in fossils (Buffre´nil V de and Quilhac A, 2021; Padian K and Lamm ET, 2013), including growth pattern, ontogenetic stage and life adaptations. The age of the organisms can be inferred through the osteohistology information. Osteohistology has contributed to our understanding of extinct creatures such as dinosaurs (Chinsamy A and Rubidge BS, 1993; Curry KA, 1999; Kohler M et al., 2012; Reid REH, 1984), parareptiles (Canoville A and Chinsamy A, 2017; Scheyer TM and Sander PM, 2009) and therapsids (Botha J, 2003, 2020; Botha J and Chinsamy A, 2000; Botha J and Smith RMH, 2007; Chinsamy A and Hurum JH, 2006; Han FL et al., 2021; Ray S and Chinsamy A, 2004; Kulik ZT et al., 2021).

2. Geological setting

Numerous fossils have been discovered near Niucun, Yushe County, Shanxi, within purplish-red mudstone layers interbedded with thick-bedded gray-green quartz sandstones (Fig. 1). These rock layers were previously classified as part of the Ermaying Formation, based on the 1∶200,000 geological map of Pingyao (J4929) and are considered to represent the middle section of Member II of the Ermaying Formation. Its age should be late Anisian according to the previous work of Liu J et al. (2018) along the Yellow River.

The Ermaying Formation consists primarily of feldspar quartz sandstone interbedded with silty mudstone (Young CC et al., 1959). There are obvious cross-bedding and typical fluvial facies in the sandstones. The surrounding rock of the fossil site in this work is purplish red mudstone with high hardness and strength (Figs. 2), also contains a small amount of sandstone lenses. Rust-red disseminated structures are developed in the sandstone, suggesting a humid and hot

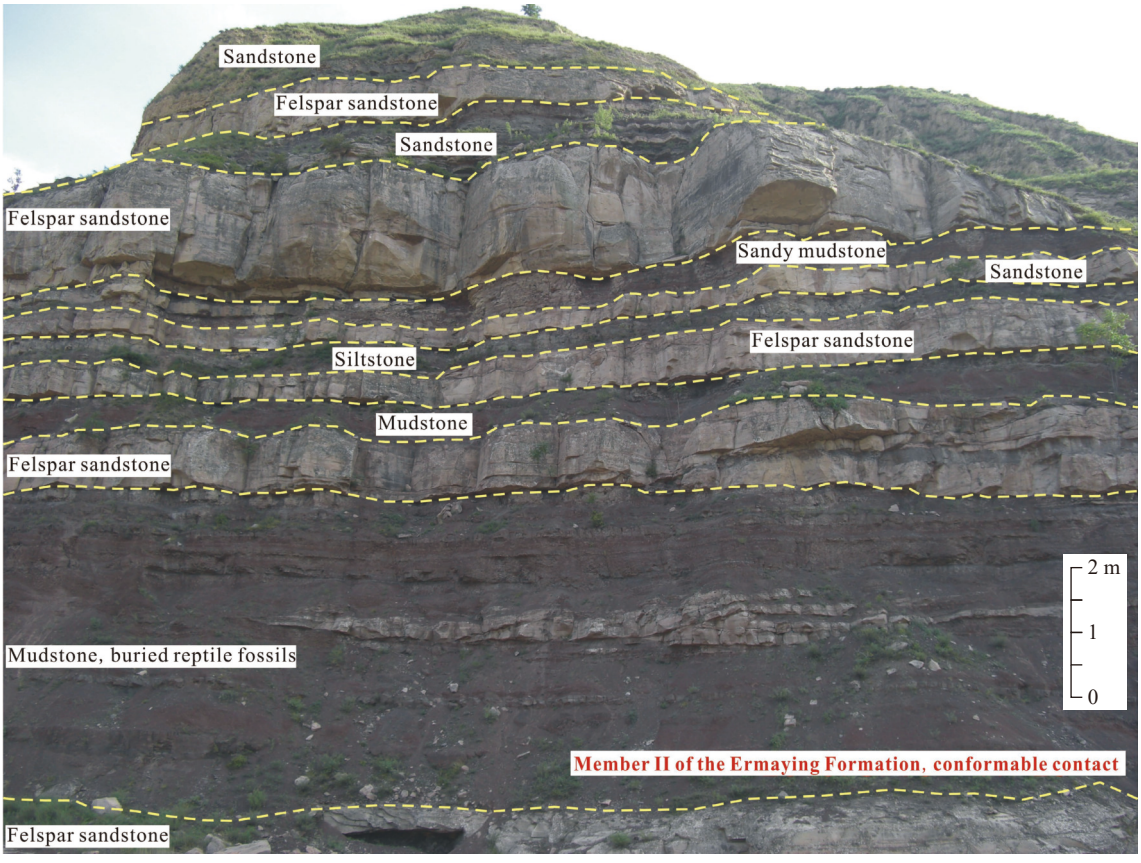

Fig. 1. Photo of Nucun locality at Yushe County, Shanxi Province, China. All tetrapod fossils from this locality come from the bottom mudstones.

climate (Dong LY, 2018; Dong LY et al., 2020; Liu J et al., 2021; Shi JR et al., 2018). The sand bodies are lenticular with some parallel bedding and unidirectional cross-bedding, shows that fluvial action is limited. The sandstone is mainly coarse feldspar quartz-sandstone with siliceous cementation. The mudstone contains numerous chert of nodules and calcareous concretion, suggesting repeated water washings (Wang RF et al., 2013). Furthermore, previous fossil evidence (Yang JS et al., 2018) and insect tracks suggest that biomass was abundant. All of these features collectively indicate that these strata were formed in an alluvial plain.

3. Methods and materials

During decades of practice work, the field team of Shanxi Museum of Geology (SXMG) summarized a pattern (Dong LY et al., 2020) that tetrapod fossils are usually buried in purplish red mudstone formed by floodplain deposits. Its overburden is a thick sandstone lens formed by channel deposition, and its present landform is usually a steep hill formed by siltstone and a gentle slope formed by underlying mudstone. The field team delineated three key regions: the Qinshui Basin in Jinzhong City, the Ningwu-Jingle Basin in Xinzhou City and the eastern coast of the Yellow River area in Lüliang City and Linfen City (Xie LJ, 2014, 2021).

In 2010, an articulated specimen was collected from the Ermaying Formation at Niucun, Yushe County (N37°07′19.1″, E112°50′26.9″). This specimen was found by Mr. Suo-zhu Wang in a 3 m thick purplish mudstone, the 20th bed in the section measured at the fossil locality (Figs. 3a–c). The restored fossil was buried *in situ*, the exposed bone structures are well preserved and most elements of skeleton is articulated, without obvious dislocation. The prepared specimen is housed in SXMG with catalogue number V 00089 (Field No. YS-077). It is identified as *Sinokannemeyeria* according to the morphological analysis below.

Histological section is made for the left femur. The femur is cut to transverse section by the automatic microtome (EXAKT 300CP). Samples is embedded in polyester resin and hardened in a light polymerization device (EXAKT 520CP) for 48 hours. Several thin sections of sample were cut by the automatic microtome (EXAKT 300CP), and then were ground and polished using the EXAKT 400CP variable speed grinding system. Images were documented using a Zeiss Axio-Cam MRc5 digital camera and Zeiss EVO 25 scanning electron microscopes (SEM) at the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP). Nomenclature and definitions of structure follow Francillon-Viellot H et al. (1990) and Chinsamy A (2012).

4. Description and comparison

The preserved skeleton of SXMG V 00089 is about 1.2 m long, and exposed in dorsal view. It contains most of the axial elements (partial skull and mandible, vertebral column and

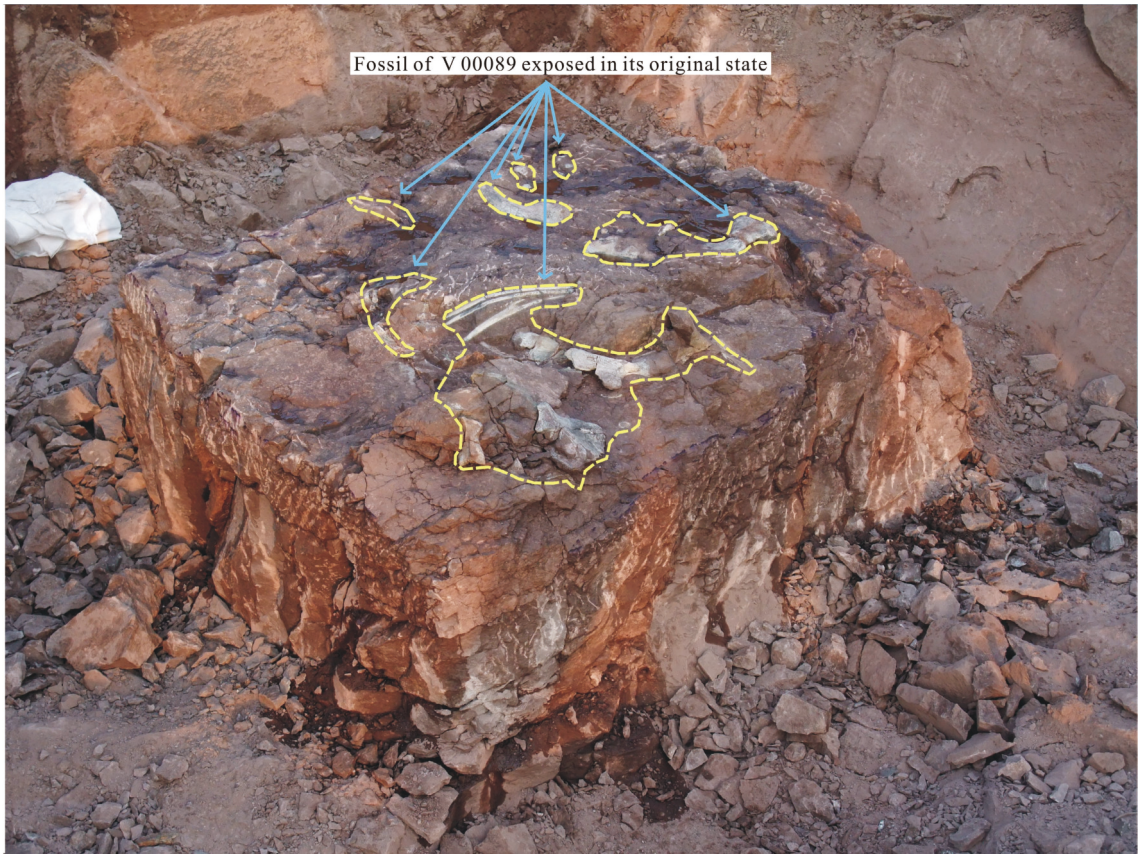

Fig. 2. Field view of SXMG V 00089 fossil specimen collection, V 00089 prior to reinforcement and packaging, its surrounding rock is purplish red mudstone with high hardness and strength.

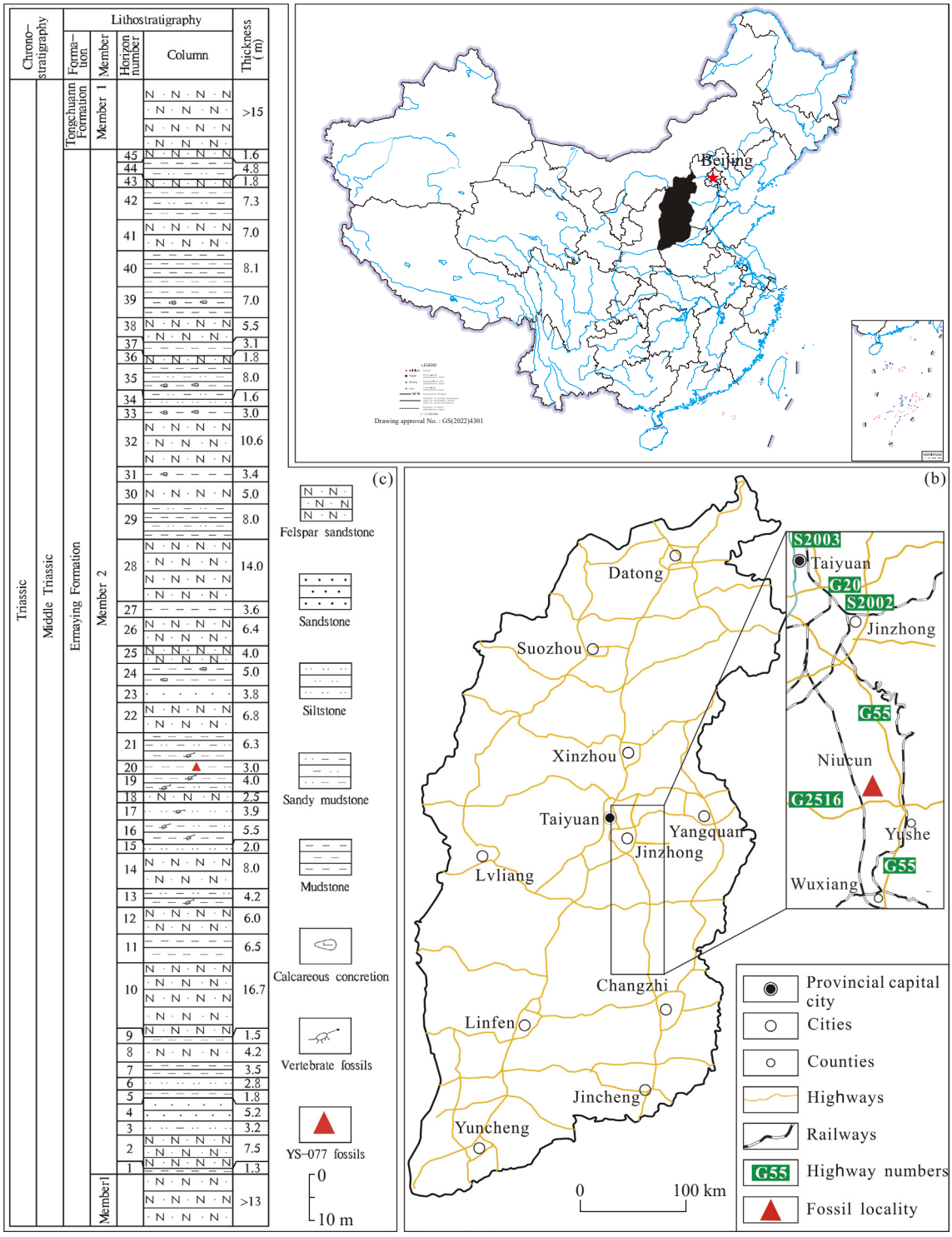

Fig. 3. Locality information for SXMG V 00089 (YS-077). a–Location of Shanxi Province, China; b–location of the fossil site; c–stratigraphical column of the specimen-bearing horizon.

ribs), pelvic girdles and nearly complete right hind limb (Fig. 4).

The skull was eroded and the dorsal portion is not preserved. The maxilla has roughened surface, projecting downward. Only the left pestle-like long tusk is connected to the caniniform process of maxilla. The tusk is stout and thick, projecting to the level below the mandible ventral edge. The maxilla process is a relative robust element. The anterior margin of the maxilla process forms an acute angle with the posterior margin. After protruding out form the alveolar, the end of tusk is slightly bending backward, forming a right angle with the posterior of maxilla (Fig. 5a). The right squamosal provides the length proportion of orbital and temporal fenestra. The infraorbital portion of squamosal is robust and the cross section of squamosal is triangular shape.

The vertebrate column and ribs are almost articulated, 11 presacral vertebrae and 8 caudal vertebrae are maintained in initial condition. The paired ilia and ischia covered the sacral vertebrae. Only the right hind limb is well preserved. The left

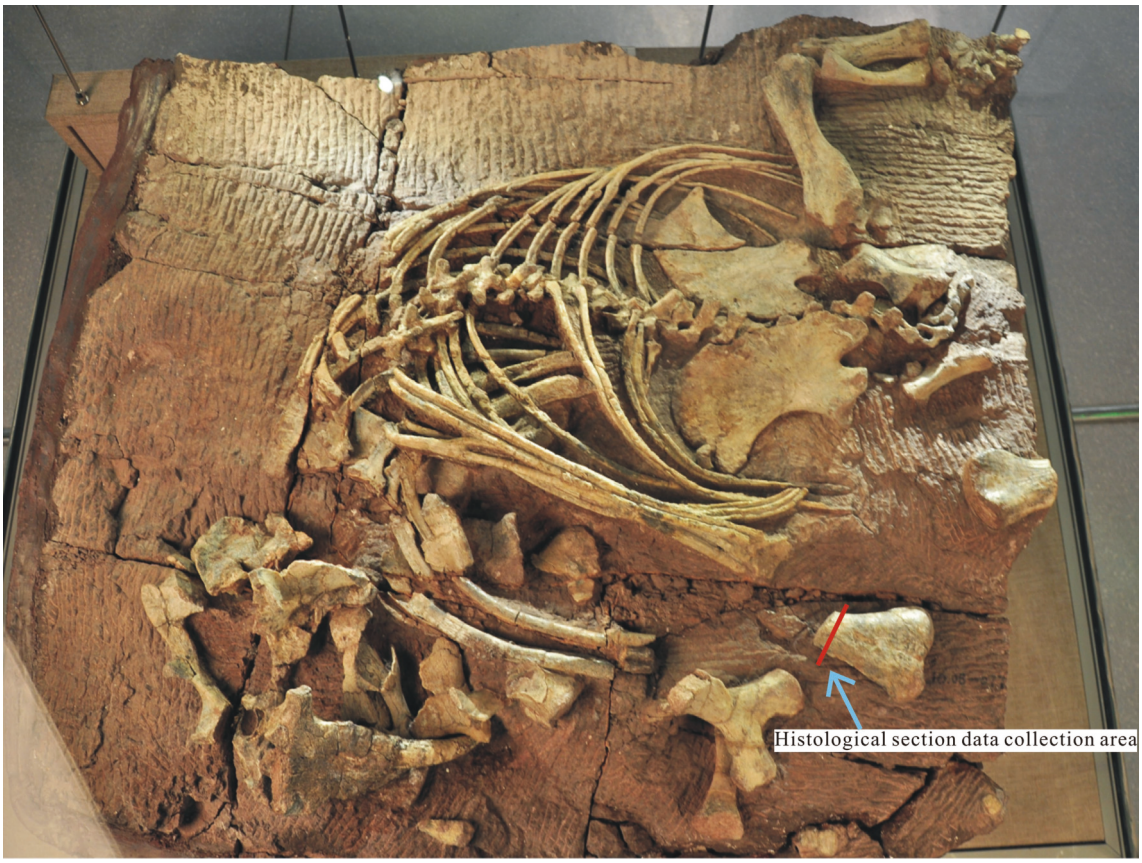

Fig. 4. Photo of SXMG V 00089 displayed in the exhibition hall of SXMG. It is nearly 0.9 m×0.9 m square in size and is stored in a rectangular glass case of 1.3 m×1 m. The red line shows the position of the histology section across the left femur.

appendicular elements are dislocated and incomplete.

The cervical elements are missed and the center of the dorsal vertebrae are indiscernible. The dorsal neural spines are directed posterodorsally, and their heights are gradually increased backwards. They are most robust in the middle section of the dorsal region. There are 14 ribs on the left and 11 ribs on the right, and their lengths are almost identical. The sacral region is fused by several vertebrae, the number of sacral vertebrae is indeterminacy due to the invisibility of medial side of both ilia. Their neural spines are blade shape and slightly projecting posterodorsally except for the last one which is considered as the first caudal vertebra.

The pelvic girdle is trident-like, with the ilium, pubic and ischium respectively directed dorsally, ventrally and ventral-caudally. The iliac blade is fan-shaped, expanding antero-posteriorly, and with slightly convex dorsal margin. The anterior process of ilium is longer and wider than the posterior one. The anterior process is pointed while the posterior process protrudes caudally. The anteroventral margin nearly forms a line with the posteroventral margin. The acetabulum is shallow and supraacetabular buttress is undeveloped.

The right pubic-ischia plate is articulated with the ilium, and forms the ventral portion of acetabulum. The pubic portion orientate ventrally and ischia portion projecting caudally. The pubis is a triangular shape element, and its anterior edge bears a pubic tubercle. Its ventral portion is incomplete. The obturator foramen lies between the pubis and ischium. The ischium expends ventrally as a thin plate, which contacts the pubis anteriorly. Posterior to the plate, the body of ischium is thickener. The posterior portion of ischium is robust and ventral margin is broken.

The head of femur is slight swelling, and proximal portion of femur flattened mediolaterally. The cross section of femur is elliptical. The tibia is straight and fibula is curved. The tibia is much more robust than fibula. The proximal portions of the femur and the fibula are poorly ossified (Fig. 5b).

5. Histology results

The cross-section of femur of SXMG V00089 is elliptical. The bone histology shows a predominance of fibrolamellar bone tissue and a high cortical porosity. The circumferential primary osteons form laminar bone and contribute most parts of cortex. A few anastomoses link 2–4 canals to form straight and irregular canals. The cortex is filled with globular and elliptical osteocyte and there are no obvious lines of arrested growth (LAGs), indicating a rapid growth phase. Furthermore, a thin layer of parallel fibered bone as a growth mark is present in the outer region of cortex, and a few secondary osteons are present in the inner cortex, suggesting slightly reduced growth rates before death. The medullary cavity is mineralized and opaqued in the microscope field (Figs. 6a–i).

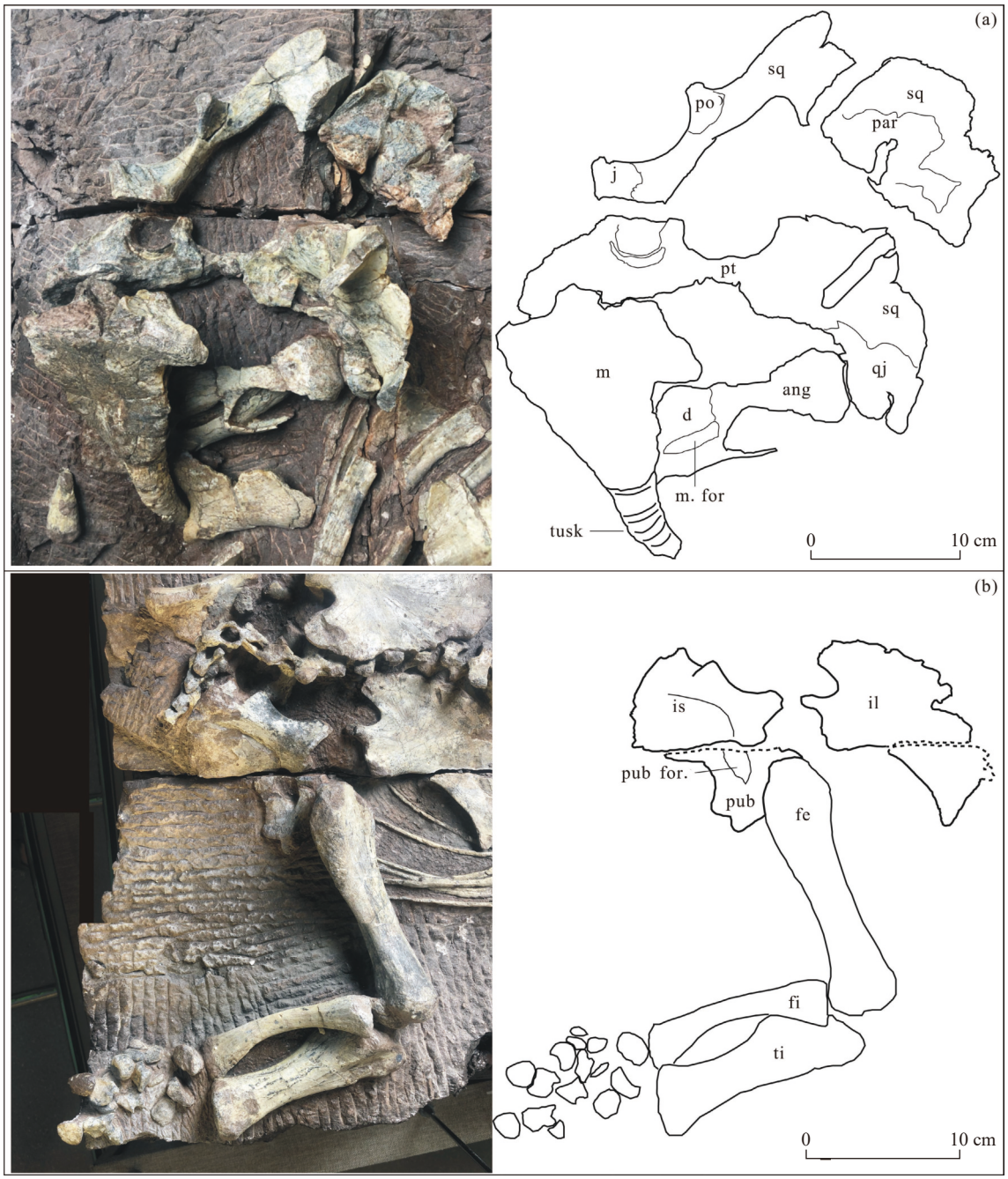

Fig. 5. Partial skeletal structure of the SXMG V 00089 in dorsal view. a–Photograph and line drawing of the skull; b–photograph and line drawing of the right pelvic girdle and right hind limb. Abbreviations: ang–angular; d–dentary; fe–femur; fi–fibula; il–ilium; is–ischium; j–jugal; m–maxilla; m. for–mandibular foramen; par–paroccipital; po–postorbital; pub–pubis; pub for–pubic foramen; pt–pterygoid; qj–quadratojugal; sq–squamosal; ti–tibia.

6. Discussion

Due to the poor preservation of the skull, it is challenging to identify diagnostic features for this specimen. For the known three kannemeyeriiform genera from Qinshui Basin, the following features are consistent with *Sinokannemeyeria* but not *Parakannemeyeria* or *Shansiodon*. These distinguishing features include a robust and ventrally directed caniniform process, a slightly posteriorly curved tusk, the temporal fenestra length at squamosal is roughly equal to the orbital length. The holotype of *Shansiodon wangi* also has a relatively long and curved tusk. However, it looks like the result of deformation. Its caniniform is much thinner and less obtuse compared to SXMG V 00089.

The orbit is relatively large as in the holotype of *Sinokannemeyeria sanchuanheensis*, indicating the juvenile state of both specimens. This is also supported by the histological features.

The microstructure of different individuals is characterized by the preponderance of highly vascularized fibrolamellar bone tissue, which constitutes the greater part of the cortex (Buffre´nil V de and Quilhac A, 2021; Padian K and Lamm ET, 2013; Ray S, 2010). Fibrolamellar bone tissue is considered to indicate rapid osteogenesis and hence an

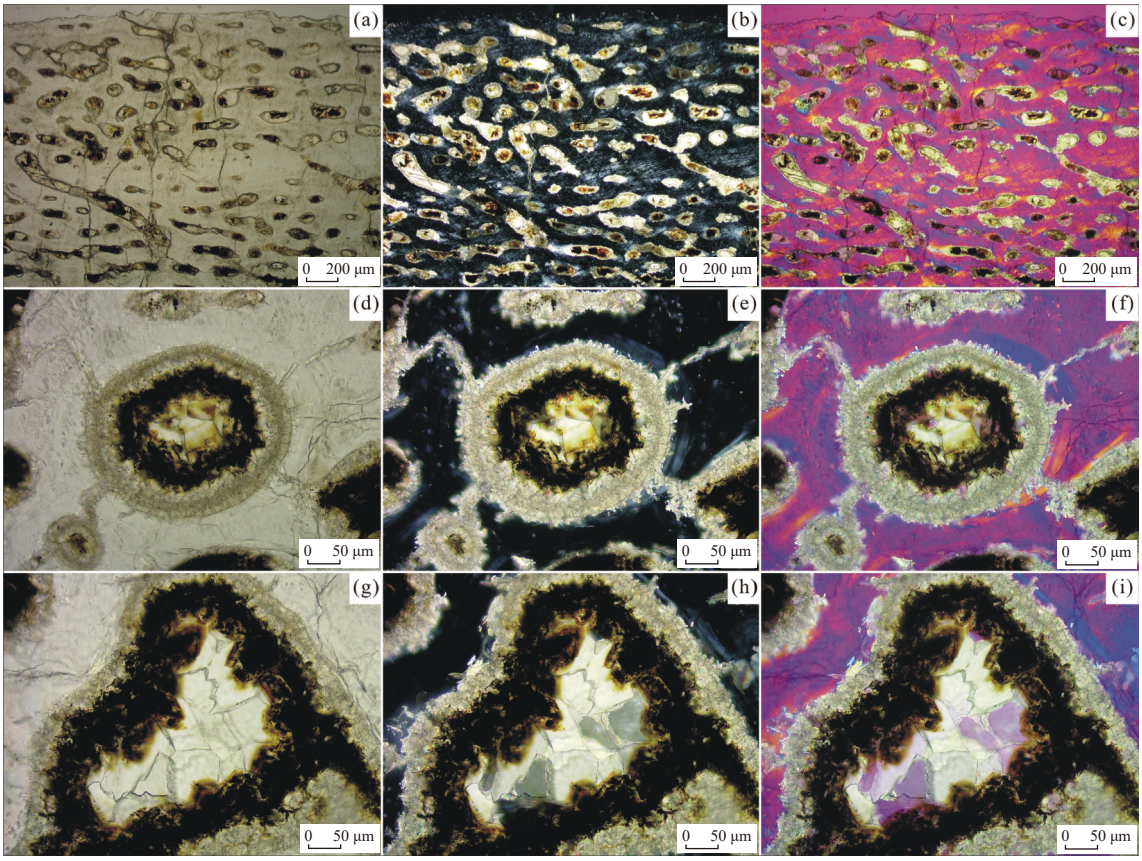

Fig. 6. Bone microstructure in juvenile SXMG V00089. a–c–The outer cortex under normal light; planepolarized light; orthogonal polarized light (scale=200 μm); d–f–the recrystallization of the endosteal cell under normal light; plane-polarized light; orthogonal polarized light (scale=50 μm); g–i–the secondary osteon in the inner cortex under normal light; plane-polarized light; orthogonal polarized light (scale=50 μm).

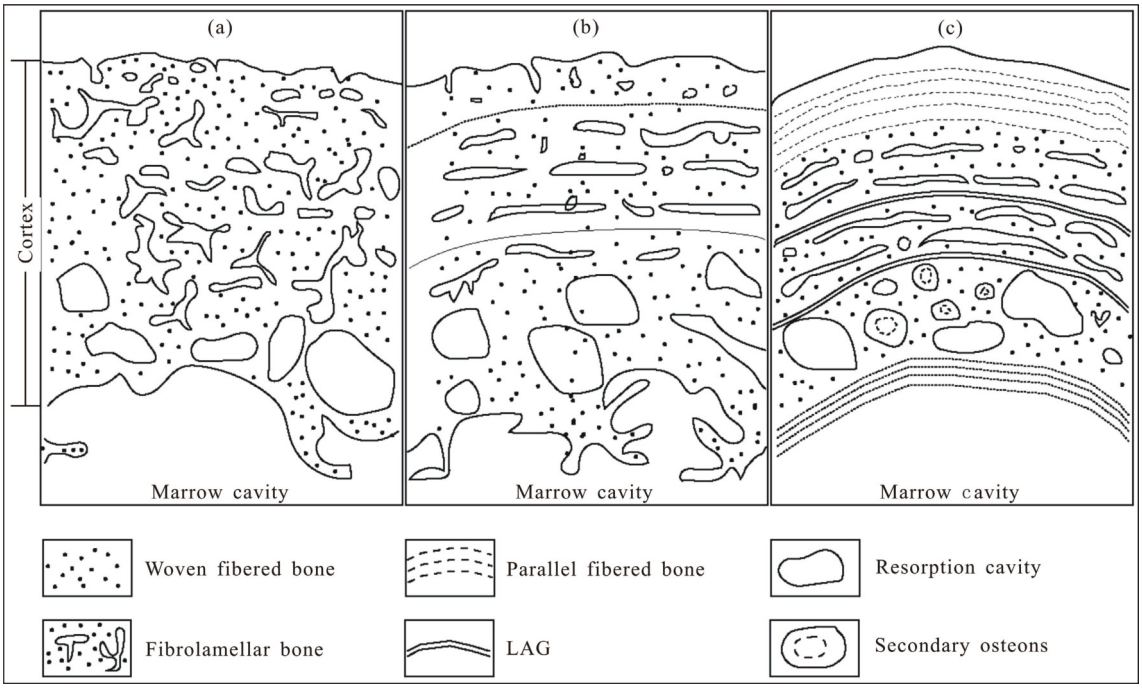

Fig. 7. Schematic representation of the bone microstructure in the three ontogenetic stages of Kannemeyeriid (after Ray S, 2010). a–The early juvenile stage; b–the late juvenile stage; c–the adult stage.

overall fast growth (Amprino R, 1947; De Margerie et al., 2002). The juvenile stage is characterized by uninterrupted fibrolamellar bone tissue in the cortex and a high cortical porosity. Growth marks and the secondary reconstruction were absent in juvenile stage (Buffre´nil V de and Quilhac A, 2021; Padian K and Lamm ET, 2013; Ray S, 2010). The

juvenile stage continues until reaching approximately 30% of adult size. After this, growth stage is interrupted periodically. The subadult stage was characterized by interrupted tissue as LAGs (Figs. 7a–c). The high prevalence of peripheral parallel fibred bone has been noted in *Oudenodon* (Botha J, 2003) and *Wadiasaurus* (Ray S, 2010). The onset of endosteal bone deposition indicates the late stage of fast growth, which continued till the 60% of adult size.

SXMG V 00089 lacks LAGs, indicating a juvenile stage, while the parallel fibered bone as a growth mark and the secondary osteons suggests a late stage of juvenile (Ray S, 2010). The growth stage initially progresses rapidly and then decreases more slowly toward the final stage. However, the other bone elements are indistinguishable from the surrounding rock. The absence of microstructure on the humerus, tibia, and fibula limits further histological analysis.

As a member of *Sinokannemeyeria*, SXMG V 00089 has two long tusk, short neck, short tail and other typical features (Figs. 8a–c). This reconstruction is based on the work of Sun AL (1963).

7. Conclusion

SXMG V 00089 was buried in the flood plain. It can be identified as *Sinokannemeyeria* based on a robust ventrally directed caniniform process, a slightly posteriorly curved tusk, and a temporal fenestra length roughly equal to the orbital length. According to the histological information, it represents a late-stage juvenile. This skeleton preserves the first juvenile skeleton of Chinese Kannemeyeriiformes.

Fig. 8. Large stone statue and reconstruction drawing of Kannemeyeriid, as the macroscopic features of V 00089. a–Lateral view of the stone statue; b–anterior view of the stone statue; c–scientifical reconstruction drawing.

CRediT authorship contribution statement

Li-juan Xie conceived the idea. Li-juan Xie and Jian Yi wrote the manuscript and prepared all the figures. Jian Yi performed the experiments. Jian-ru Shi and Run-fu Wang managed the project, Shi-chao Xu, Zhi-shuai Kang participated the field work. All authors reviewed the manuscript.

Declaration of competing interest

The authors declare no conflicts of interest.

Acknowledgements

This work was jointly supported by Department of Natural Resources of Shanxi Province and the Strategic Priority Research Program of Chinese Academy of Sciences (XDB26000000).

The authors are grateful to Zhi-lu Tang of IVPP and Xiao-chun Wu of Canadian Museum of Nature (CMN) for their assistance in all stages of this work, to Suo-zhu Wang of SXMG for his remarkable work in the field, to Yu-qing Zhang for his skillful preparation on the specimen, to Ran Guo of SXMG for photography, to Jun Liu and Qi Zhao of IVPP for valuable comments, to Yu-tai Shi of IVPP for improvement of writing, to the Assess Committee of Chinese Vertebrate Paleontological Experts for support. The authors also appreciate two anonymous referees carefully reviewed the manuscript, offering critical comments and suggestions that led to its great improvement.

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