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The discovery of a large ceratodontiform lungfish from the Middle Triassic (Anisian) of Shanxi, China

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Abstract Ceratodontiformes is the only extant order of Dipnoi (lungfishes). Fossil remains of this group are rare in Triassic deposits in China. Here, we report the recent discovery of a large ceratodontiform lungfish from the Anisian (Middle Triassic) *Sinokannemeyeria* Fauna in the Taigu District of Jinzhong City, Shanxi Province, China. The specimen was preserved in the argillaceous siltstones from the Third (uppermost) Member of the Ermaying Formation, including remains of 20 caudal vertebrae and associated elements ('supraneurals', interhaemals and dorsal and ventral radials) as well as a series of dorsal fin rays. The discovery documents the oldest articulated ceratodontiform in East Asia, predating the previously known articulated ceratodontiform from the Early Jurassic Yuzhou Biota by at least 43 Ma. With an estimated length of ~162 cm, it represents the largest articulated ceratodontiform known so far in the Triassic. The new finding adds to our knowledge regarding body size, morphological diversity, and the paleogeographic distribution of early ceratodontiforms.

Key words Jinzhong, Shanxi; Middle Triassic; Ceratodontiformes; *Sinokannemeyeria* Fauna

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1 Introduction

Lungfishes (Dipnoi) are a lineage of sarcopterygians (lobe-finned fishes) which are known from the Early Devonian to present. Although they are represented by only three genera alive today in the South Hemisphere, i.e., *Protopterus* in Africa, *Leipdosiren* in South America, and *Neoceratodus* in Australia, this lineage was much more diverse in the fossil record and had a global distribution during the Paleozoic and Mesozoic (Miles, 1977; Nessov and Kaznyshkin, 1985; Campbell and Barwick, 1990; Schultze, 2004; Cavin et al., 2007; Kemp et al., 2017).

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Taxonomically, Mesozoic and Cenozoic lungfishes are referred to the order Ceratodontiformes (Nelson et al., 2016). In the Triassic, ceratodontiforms have been extensively documented from the Gondwanan continental and marine shelf deposits of Madagascar, Africa (Teixeira, 1949; Lehman et al., 1959; Beltan, 1968; Martin, 1979), Australia (Ritchie, 1981; Kemp, 1994, 1998), India (Jain, 1968), Antarctica (Dziewa, 1980) and South America (Agnolín et al., 2017). They also exist from Laurasian landmasses including Europe (Schultze, 1981; Skrzycki et al., 2018), North America (Case, 1921; Rose et al., 2024), central and eastern Asia (Vorobyeva, 1967; Cheng, 1980; Martin and Ingavat, 1982), and Middle East (Kear et al., 2010). The Triassic ceratodontiform fossils are characterized by an abundance of highly mineralized tooth plates, whereas cranial and postcranial remains are relatively scarce.

Here, we report the discovery of a large ceratodontiform lungfish based on postcranial material from the Middle Triassic continental (fluvial or lacustrine) deposits of Shanxi Province, China. The specimen, although incomplete, has an estimated length of ~162 cm, representing the largest articulated ceratodontiform known so far in the Triassic. The fossil was preserved in the argillaceous siltstones from the Third (Upper) Member of the Ermaying Formation exposed in the Taigu District of Jinzhong City (Fig. 1). Besides the lungfish, a prolific terrestrial tetrapod assemblage (*Sinokannemeyeria* Fauna), invertebrates, and plants

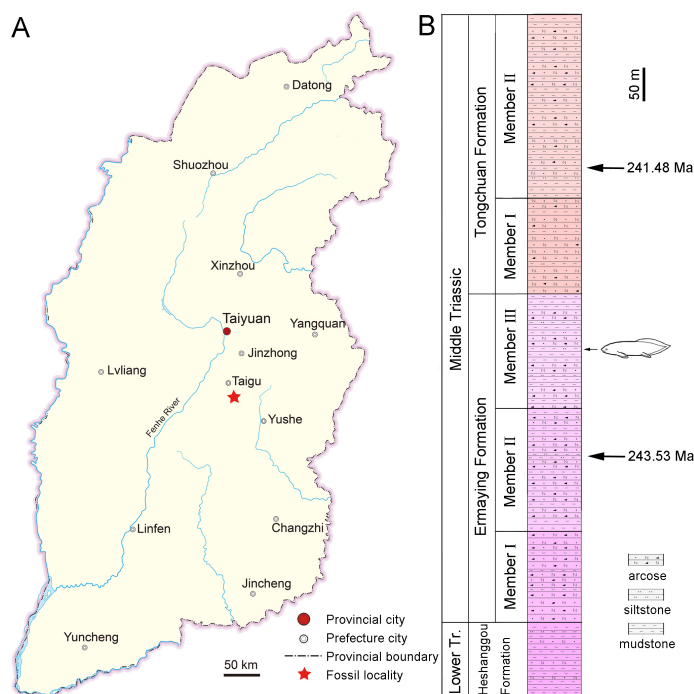


Fig. 1 Fossil locality and stratigraphic section of the lungfish from the Middle Triassic (Anisian) of Jinzhong, Shanxi, China

A. locality map; B. stratigraphic section. U-Pb geochronologic ages from Liu et al. (2018)

Map approved number: GS(2019)3333

have also been recovered from these fossil beds (Cheng, 1980; Liu et al., 2018). The age of the fossil beds has been well constrained to the late Anisian (~242 Ma) by both biostratigraphic correlation and U-Pb dating (Liu et al., 2018). Consequently, the new finding represents the oldest articulated ceratodontiform in East Asia (see Discussion below).

2 Materials and methods

The studied material of the ceratodontiform is stored in the fossil collections of the Shanxi Natural History Museum (formerly Shanxi Museum of Geology Taiyuan, SXMG) in Taiyuan, Shanxi (Fig. 1). It was prepared by air-chisels, accompanied with sharp steel needles. The specimen was photographed in its original state with a Canon 800D digital camera, and the line-drawing was made from tracings of photographs. The description of the postcranial skeleton follows the terminology used by Arratia et al. (2001), who suggested that the ‘supraneural’ bones in dipnoans and other sarcopterygians are probably not homologous to those in actinopterygians. In some previous descriptions of dipnoans, the ‘supraneural’ was also named ‘lower interneural’ (Günther, 1871), ‘proximal radial’ (Cloutier, 1996), or ‘distal supraneural’ (Ahlberg and Trewin, 1995).

3 Systematic paleontology

Subclass Sarcopterygii Romer, 1955

Superorder Dipnoi Müller, 1845

Order Ceratodontiformes Berg, 1940

Family, Genus and Species indet.

(Fig. 2A, B)

Referred specimen SXMG V2038. Remains of 20 caudal vertebrae and associated elements.

Locality and horizon Taigu District, Jinzhong City, Shanxi Province. Third (Upper) Member of the Ermaying Formation. Anisian, Middle Triassic.

Description The specimen is large but incomplete with the head, trunk and paired fins missing. The remains include the caudal region of the vertebral column with associated elements (‘supraneurals’, interhaemals and dorsal and ventral radials) and a series of dorsal fin rays. There are in total 11 neural spines, 18 ‘supraneurals’, 17 dorsal radials, nine haemal spines, and nine interhaemals preserved in the specimen; ossified centra are clearly absent. These bones correspond to 20 caudal vertebrae, and for convenience in the following description, they are numbered in sequential order (Fig. 2). The preserved length of the whole specimen is 38 cm from the proximal end of the first dorsal radial to the distal end of the 20th interhaemal. According to the body-length ratio of the ceratodontiform *Paraceratodus germaini* based on nearly complete specimens from the Early Triassic of Madagascar (Lehman

et al., 1959), this Chinese ceratodontiform is estimated to have a total body length (TL) of ~162 cm.

The 13th to 15th vertebrae neural arches are the best preserved (Fig. 2B). As in extant adult ceratodontiform, the neural arches are short, paired elements that are fused distally with the median neural spine. The neural arches form a forked structure near the base of the neural spine and leave a small median place that would contain the spinal cord as in extant lungfishes (Fig. 2E). Among the 11 preserved neural spines, the posterior eight were nearly completely preserved. They are rod-like with an expanded distal end, and their length gradually reduces posteriorly. The 12th neural spine (plus arches) is three times as long as the 20th neural spine (plus arches).

The ‘supraneurals’ are situated dorsal to the neural spine. The proximal portions of several anterior (3rd to 7th) ‘supraneurals’ are missing, and the 8th to 19th ‘supraneurals’ are complete and gradually reduce in length posteriorly. The ‘supraneurals’ are rod-like and expanded at both ends. They are longer than the corresponding neural spine; for example, the 13th neural spine is 63.6% the length of the 13th ‘supraneurals’.

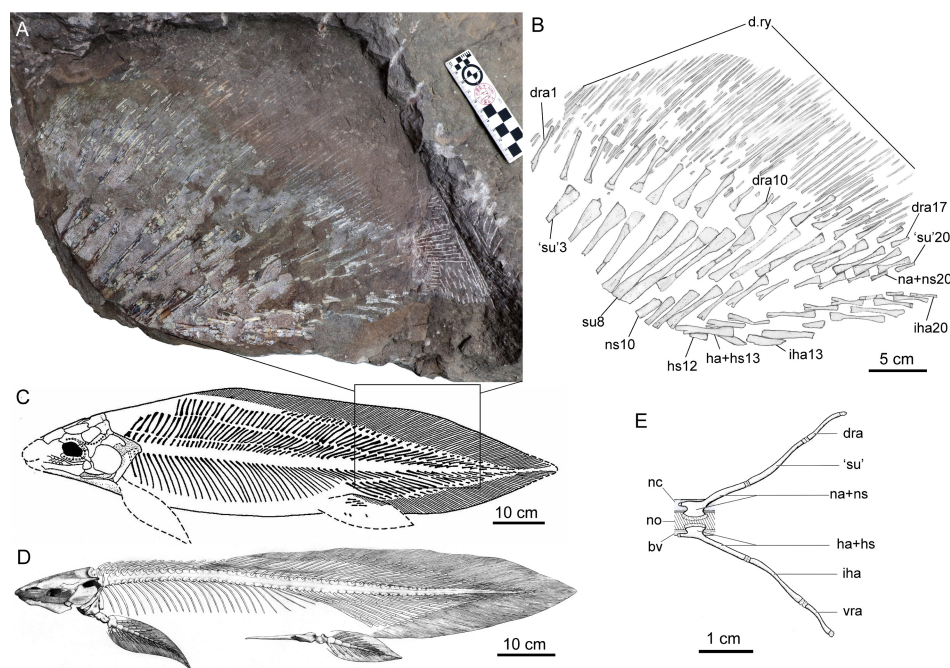


Fig. 2 Vertebral column with associated elements and fin rays of the ceratodontiform from the Middle Triassic of Shanxi Province and comparison with those of other ceratodontiforms

A, B. photo (A) and line-drawing (B) of SXMG V2038; C. reconstruction of *Paraceratodus germaini* from the Lower Triassic of Madagascar (from Schultze, 2004) with a square indicating the area comparable to the specimen from Shanxi, China; D. skeleton and fins of extant *Neoceratodus* from Queensland (from Günther, 1871); E. caudal vertebra of extant *Lepidosiren* from South America (modified from Arratia et al., 2001) Abbreviations: bv. blood vessels; dra. dorsal radial; d.ry. dorsal fin ray; ha. haemal arch; hs. haemal spine; iha. interhaemal; na. neural arch; nc. spinal cord; no. notochord; ns., neural spine; 'su'. 'supraneural'; vra. ventral radial

There are 17 dorsal radials preserved distally to the ‘supraneurals’. They are also rod-like and about half the length of the corresponding ‘supraneural’. Both ends of the radials are expanded, with the proximal end more conspicuously expanded. The anterior 10 radials are nearly equal in length, and the other radials (12th to the 17th) gradually reduce in length posteriorly. The fin rays are long and numerous with their unsegmented proximal portions inserting between the radials. It is unknown whether or not the distal portions of the rays are segmented, as in extant lungfishes, because of the poor state of preservation.

The 13th to 20th haemal spines are relatively well-preserved. The paired haemal arches are fused distally with the corresponding haemal spine, and resemble the neural arches and spines in shape and size. Nine interhaemals are located distally to the haemal spines. Among them, the posterior five interhaemals (16th to 20th) are nearly complete. They are also rod-like and gradually reduce in length posteriorly. The ventral radials and rays are missing because of incomplete preservation.

4 Discussion

The morphology of the vertebral column and associated elements of this new specimen shows a similar pattern of bony elements as those found in Early Triassic fossil (e.g., *Paraceratodus* and *Gosfordia*) and living ceratodontiforms (Lehman et al., 1959; Kemp, 1994; Arratia et al., 2001). This supports the attribution of the taxon to the Ceratodontiformes. Notably, the presence of a series of ‘supraneurals’ between the neural spines (plus arches) and radials in the caudal region is autapomorphic for lungfishes (Arratia et al., 2001). However, the ceratodontiform lungfish described herein cannot be identified at the genus or species level because of the absence of any information regarding the skull. To our knowledge, the new finding represents the largest articulated ceratodontiform from the Triassic. The previous largest known articulated ceratodontiform was represented by *Paraceratodus germaini* from Madagascar with a TL of 103 cm (Lehman et al., 1959). Other articulated ceratodontiforms based on nearly complete specimens are represented by *Gosfordia truncata* and *Ariguna formosa* from the Early Triassic of Australia (Kemp, 1994), but they are smaller, having a TL of 50 and 10.5 cm, respectively. Additionally, the TLs of some Triassic genera based only on skull bones can also be estimated, including *Ptychoceratodus serratus* from the Middle Triassic of Switzerland and Germany, *Arganodus atlantis* from the Late Triassic of Morocco, and *Ceratodus sturii* from the Late Triassic of Austria (Kemp, 1998). Among these, the largest one is *P. serratus* with a head length (HL) of ~23 cm, which is somewhat smaller than *P. germaini* (HL= 26 cm, TL= 103 cm; Lehman et al., 1959). Based on this measurement, *P. serratus* is estimated to have a TL of slightly less than 100 cm, which is notably smaller than that of the ceratodontiform fossil (TL: ~162 cm) reported here.

Fossil ceratodontiforms are rare from the Triassic of China. Previous record consisted of

a single small tooth plate (*Ceratodus heshanggouensis*) from the Early Triassic Heshanggou Formation in Lvliang, Shanxi (Cheng, 1980). The new finding from Jinzhong represents the second record of Chinese ceratodontiforms in the Triassic and the only ceratodontiform record known from the Middle Triassic (~242 Ma; Liu et al., 2018) of East Asia. Furthermore, it represents the oldest articulated ceratodontiform in China or even in all of East Asia. The previously oldest known articulated ceratodontiforms from this region were recovered from the Early Jurassic (Sinemurian, ~193–199 Ma) Yuzhou Biota in northern Chongqing, southwestern China (Ren et al., 2024). The new discovery predates the previous record of articulated ceratodontiforms in East Asia by at least 43 Ma and provides additional information for our understanding of the morphology, size, and distribution of early ceratodontiforms.

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山西中三叠世安尼期一大型角齿鱼目肺鱼

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摘要: 角齿鱼目是肺鱼超目中唯一包括现生成员的目级单元, 其化石少见中国三叠纪地层。最近在山西省中三叠世安尼期中国肯氏兽动物群发现一种大型角齿鱼目肺鱼。化石保存于晋中市太谷区二马营组第三段(最上段)的泥质粉砂岩中, 包括20块尾椎骨及相关的“上神经骨”, 间椎骨和背、腹辐鳍骨和一系列背鳍条。它代表了东亚已知最古老的、保持自然连接状态的角齿鱼目化石, 比此前在早侏罗世渝州生物群发现的角齿鱼目化石至少早43 Ma。据估计, 该肺鱼体长约为162 cm, 是迄今已知三叠纪最大的、自然连接状态的角齿鱼目化石。这一发现增加了对早期角齿鱼目体型大小、形态多样性和古地理分布的认识。

关键词: 山西晋中, 中三叠世, 角齿鱼目, 中国肯氏兽动物群

中图法分类号: Q915.862 文献标识码: A 文章编号: 2096-9899(2026)02-0183-08

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