

DOI: 10.19615/j.cnki.1000-3118.191105

A redescription of the Silurian *Sinogaleaspis shankouensis* (Galeaspida, stem-Gnathostomata) from Jiangxi, China

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Abstract *Sinogaleaspis shankouensis* is redescribed based on 11 new specimens collected from the type locality of the Xikeng Formation in Xiushui county, Jiangxi Province. The in-depth morphological study indicates that the sensory canal system of *S. shankouensis* exhibits a mélange of characters of plesiomorphic galeaspid taxa, Eugaleaspiformes, Polybranchiaspiformes and Huananaspiformes. The grid distribution of the sensory canal system on the dorsal side of the head-shield, which comprises four longitudinal canals intercrossed with six pairs of transverse canals in *S. shankouensis*, probably represents a plesiomorphic condition of vertebrates. *Sinogaleaspis shankouensis* belongs to the *Sinogaleaspis-Xiushuiaspis* Fauna or the Maoshan Assemblage which represents the first diversification of galeaspids in the Telychian, Llandovery of the Silurian period. The sedimentary paleoenvironment of the Xikeng Formation in Xiushui, Jiangxi Province is suggestive of a brackish water environment, whereas a large sum of muddy gravels in fish-bearing sandstone beds point to a short distance of potamic transportation. This indicates that the *Sinogaleaspis-Xiushuiaspis* Fauna may live in a fresh water environment in the river rather than their burial area in the sea.

Key words Xiushui, Jiangxi; Silurian; eugaleaspids, *Sinogaleaspis*; sensory canal system

Citation Gai Z K, Shan X R, Sun Z X et al., 2020. A redescription of the Silurian *Sinogaleaspis shankouensis* (Galeaspida, stem-Gnathostomata) from Jiangxi, China. *Vertebrata Palasiatica*, 58(2): 85–99

1 Introduction

Sinogaleaspis, the type genus of the family Sinogaleaspidae, comprises two species, *S. shankouensis* and ‘*S. xikengensis*’ (Pan and Wang, 1980). The monophyly of the

中国科学院前沿科学重点研究计划(编号: QYZDB-SSW-DQC040, QYZDJ-SSW-DQC002)、国家自然科学基金(批准号: 41572018, 41530102, 41972006)、国家高层次人才特殊支持计划(万人计划)、中国科学院战略性科技先导专项(编号: XDB26000000)、现代古生物学和地层学国家重点实验室(中国科学院南京地质古生物研究所)和“中国科学院大学生创新实践训练计划”项目资助。

收稿日期: 2019-09-06

Sinogaleaspidae remains controversial largely due to the poorly known nature of *S. shankouensis* whose description was based on two incomplete specimens from the Lower Silurian of Xiushui, Jiangxi Province (Pan, 1986a; Zhu, 1992; Gai et al., 2005, 2018; Gai and Zhu, 2005, Zhu and Gai, 2006, Liu et al., 2015). Among about 80 described galeaspid species, the sensory canal system of *S. shankouensis* is peculiar in bearing three pairs of median transverse canals, which contrasts with the known pattern of other galeaspid (Liu, 1986; Wang, 1991; Liu et al., 2015; Gai and Zhu, 2017). Considering the unusual condition known from two poorly preserved specimens, Wang (1991) pointed out that the present interpretation of the sensory canal system in *S. shankouensis* needs further corroboration from additional materials. Since 2003, the authors have organized five field excursions to the type locality of *S. shankouensis*, i.e. Xikeng village of Xiushui, Jiangxi Province, and collected abundant fish remains including 11 new specimens of *S. shankouensis*. Based on these new data, we present a detailed redescription of *S. shankouensis*, and clarify its sensory canal condition.

2 Geological setting

The new material of *Sinogaleaspis shankouensis* was collected from the type locality of the Xikeng Formation in Taiyangshen Town, Xiushui County, Jiangxi Province, South China (Fig. 1A). The fish-bearing Xikeng Formation belongs to the Upper Red Beds (URBs) in South China, which is equivalent of the Huixingshao Formation in Chongqing and Guizhou, and the Maoshan Formation in Jiangsu and Zhejiang. Although the precise age of URBs in western part of the Yangtze Platform is difficult to determine, an age of the middle-late Telychian is proposed in light of the evidence from the underlying Xiushan Formation with its invertebrate fauna and sequence stratigraphic analyses (Bureau of Geology and Mineral Resources of Jiangxi Province, 1984; Zhao et al., 2009; Zhao and Zhu, 2010; Wang et al., 2018; Rong et al., 2019). The Xikeng Formation in the type locality has been remeasured (Fig. 1B) as following:

Xikeng Formation (Layers above Layer 11 are not measured)

- | | |
|---|---------|
| 11. Grey-green medium-bedded siltstone, intercalated with grey-green thin-bedded silty mudstone | 10.30 m |
| 10. Purple medium and thick-bedded pelitic siltstone, intercalated with thin-bedded mudstone | 12.11 m |
| 9. Grey-green medium and thick-bedded siltstone, with abundant tiny tubular trace fossils | 1.05 m |
| 8. Yellow-green medium to thick-bedded pelitic siltstone | 5.04 m |
| 7. Purple medium and thick-bedded pelitic siltstone | 1.33 m |
| 6. Grey-green medium-bedded pelitic siltstone, intercalated with yellow-green thin-bedded mudstone | 1.81 m |
| 5. Yellow-green medium and thick-bedded siltstone, intercalated with thin and medium-bedded pelitic siltstone | 2.37 m |

4. Purple thin to thick-bedded pelitic siltstone 4.73 m
3. Grey-green thin and medium-bedded pelitic siltstone interbedded with a large sum of muddy gravels, yielding galeaspids: *Sinogaleaspis shankouensis*, '*S.* *xikengensis*', *Xiushuiaspis jiangxiensis*, and *X. ganbeiensis* 0.93 m
2. Yellow-green medium-bedded siltstone 1.27 m
1. Purple thin and medium-bedded pelitic siltstone, intercalated with thin-bedded mudstone 25.02 m
- conformity ——
- Xiajiaqiao Formation
0. Medium and thick-bedded fine sandstone 1.31 m

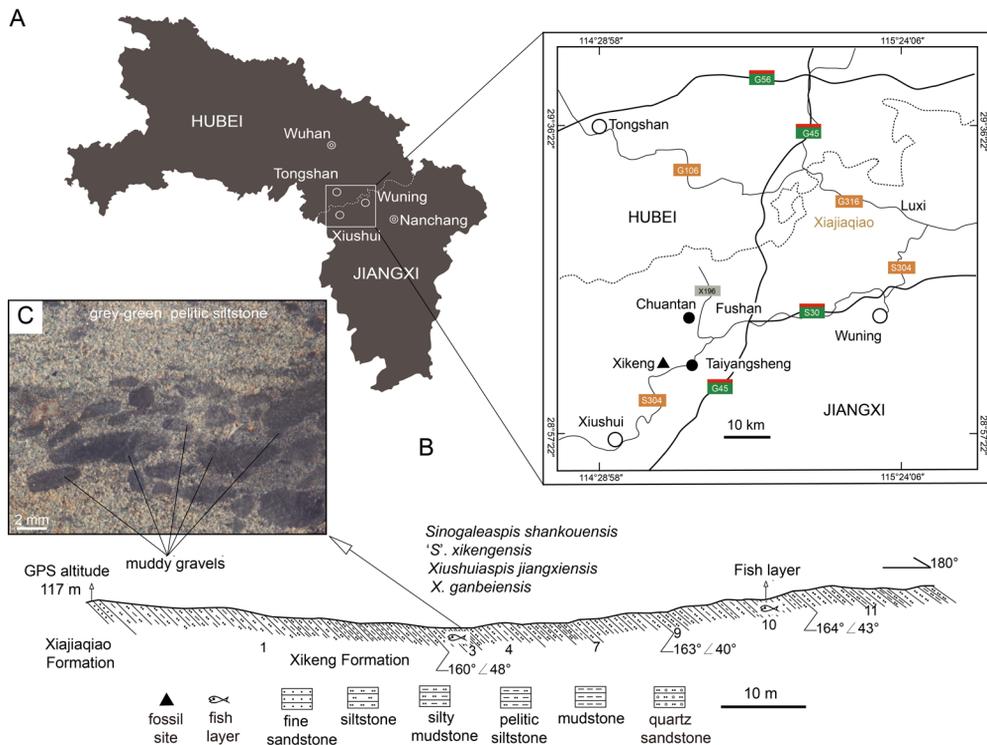


Fig. 1 Geological background of *Sinogaleaspis shankouensis*

A. location map of the fossil site in Xiushui, Jiangxi, South China

B. stratigraphical section of the Xikeng Formation at the type locality

C. cross section of the fish layer showing a large sum of muddy gravels in grey-green pelitic siltstone

3 Material and methods

The new material of *Sinogaleaspis shankouensis* includes 11 head-shields (IVPP V 25135.1–11) from the type locality of the Xikeng Formation in Taiyangshen town, Xiushui county, Jiangxi Province, South China. All these specimens are permanently housed and accessible for examination in the collections of the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences (IVPP). The holotype and paratype of *S. shankouensis*, GMC V 1751 and GMC V 1752 is examined for comparison and

measurement, which is housed in the collections of the Geological Museum of China (GMC). All fossil specimens were prepared mechanically using a vibro tool with a tungsten-carbide bit or a needle. They were measured with a digital vernier calliper, studied under optical zoom, and photographed with a Canon EOS 5D Mark III camera coupled with a Canon macro photo lens (MP-E 65 mm 1:2.8 1-5×).

4 Systematic paleontology

Subclass Galeaspida Tarlo, 1967

Order Eugaleaspiformes (Liu, 1965) Liu, 1980

Family Sinogaleaspidae Pan & Wang, 1980

Genus *Sinogaleaspis* Pan & Wang, 1980

(Figs. 2–6)

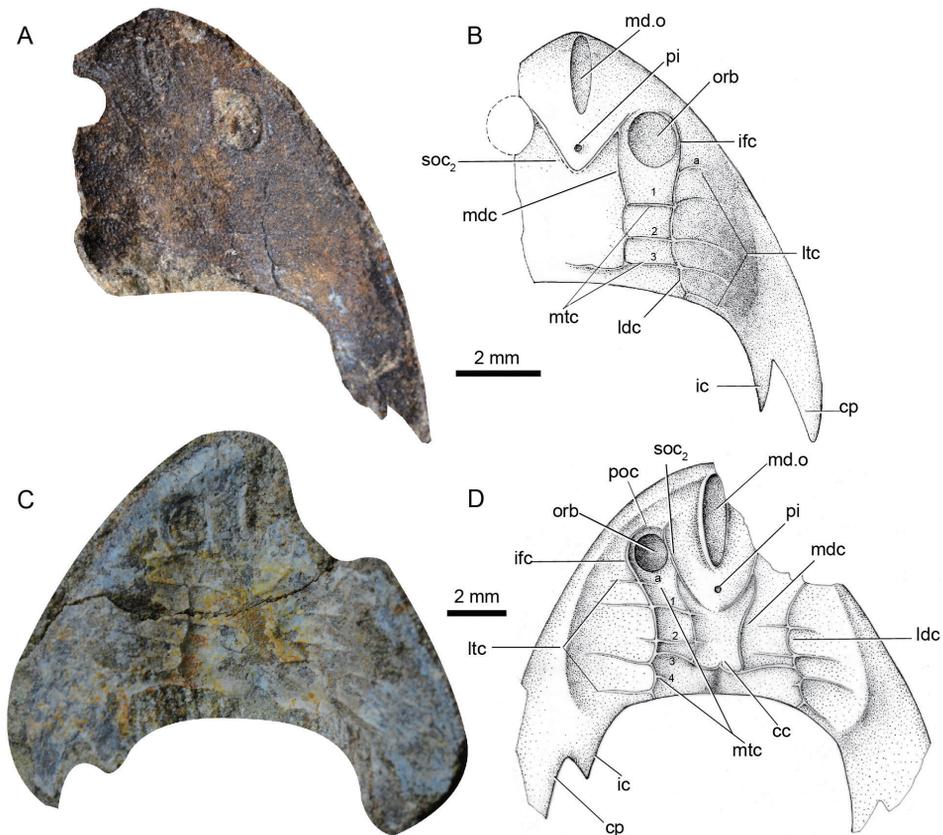


Fig. 2 Photographs (A, C) and interpretative drawings (B, D) of *Sinogaleaspis shankouensis*
A, B. IVPP V 25135.10; C, D. IVPP V 25135.6

Abbreviations: a. the first lateral transverse canal or median transverse canal issuing from infraorbital canal;
1–4. the first to fourth lateral transverse canal or median transverse canal issuing from lateral dorsal canal;
cc. central canal; cp. cornual process; ic. inner cornual process; ifc. infraorbital canal; ldc. lateral dorsal canal;
ltc. lateral transverse canal; mdc. median dorsal canal; md.o. median dorsal opening;
mtc. median transverse canal; orb. orbital opening; pi. pineal opening; poc. preorbital commissure;
soc₂. posterior supraorbital canal

Diagnosis (emended) A small-sized sinogaleaspid jawless fish, subtriangular head-shield with an arciform rostral margin, maximum length of head-shield about 15–18 mm, maximum width of head-shield about 17–21 mm, wider than long; cornual process developed, projecting caudo-laterally; inner cornual process spine-like, projecting caudally, much smaller than cornual process; median dorsal opening wedge-shaped or longitudinal oval in outline, its anterior end separated from the rostral margin of head-shield by a short distance, and its posterior end extending posteriorly beyond the level of the center of the orbital opening; orbital opening large, round, and dorsally positioned; pineal opening small, oval in shape, and located behind the posterior margin of the orbital opening; sensory canal system sophisticated, V-shaped posterior supraorbital canals, infraorbital canal posteriorly connected with lateral dorsal canals naturally; U-shaped medial dorsal canals joining posterior supraorbital canals anteriorly; 6 pairs of lateral transverse canals with two pairs issuing from infraorbital canals; 6 pairs of median transverse canals with the first pair the preorbital commissures uniting the infraorbital and posterior supraorbital canals in front of orbital openings; margin of head-shield smooth; ornamentation composed of tiny granular tubercles decreasing gradually from the shield center towards the cornual process.

***Sinogaleaspis shankouensis* Pan & Wang, 1980**

(Figs. 2–6)

Sinogaleaspis shankouensis Pan and Wang, 1980, p. 3, fig. 3, pls. I, II

Sinogaleaspis shankouensis Liu, 1986, p. 248, fig. 2A

Sinogaleaspis shankouensis Wang, 1991, p. 54, fig. 15

Sinogaleaspis shankouensis Gai et al., 2005, p. 68

Sinogaleaspis shankouensis Zhu and Gai, 2006, p.7, fig. 4D

Sinogaleaspis shankouensis Liu et al., 2015, p. 170, fig. 82

Sinogaleaspis shankouensis Gai and Zhu, 2017, p. 227, figs. 7-44, 7-45

Holotype A nearly complete head-shield, GMC V 1751.

Paratype A nearly complete head-shield, GMC V 1752.

Referred specimens Two nearly complete head-shields, IVPP V 25135.1, V 25135.9, and nine incomplete head-shields, V 25135.2–8, V 25135.10–11.

Type locality and horizon Xikeng village, Taiyangshen Town (previously known as Sandu Town), Xiushui county, Jiangxi Province, China; Xikeng Formation, Telychian, Llandovery, Silurian.

Diagnosis The only known species, diagnosis as that of the genus. *Sinogaleaspis xikengensis* (Pan and Wang, 1980) is removed out of *Sinogaleaspis* as discussed below (Gai et al., 2005).

Measurements See Table 1.

Description *Sinogaleaspis shankouensis* is a small-sized sinogaleaspid jawless fish with a subtriangular head-shield (Figs. 2–6). The rostral margin of the head-shield is arciform without rostral process. The measurements of 11 specimens of *S. shankouensis* indicate that the size of

the head-shield is quite stable with the maximum length of head-shield varying from 15.5 mm to 18.4 mm, the maximum width of head-shield varying from 17.2 to 20.8 mm, and the length of head-shield in midline varying from 9.6 to 12.7 mm (Table 1). There are about 10% variation in the size of head-shield. The head-shield is wider than it is long. Caudally, the head-shield protrudes into a pair of cornual and inner cornual processes. The cornual processes, which are completely preserved in V 25135.1, 3, 4, 9, are oriented caudo-laterally (or postero-laterally), short and rapidly tapered off (cp, Figs. 2, 3A–C, E, 4A, B). The inner cornual processes, which are completely preserved in V 25135.1, 3, 6, 9, are small and spine-like, projecting caudally (ic, Figs. 2, 3A–C, 4A, B). The inner cornual processes are much smaller than the cornual processes.

The median dorsal opening (md.o, Figs. 2–6) is fairly long, wedge-shaped or elliptic in outline with long axis aligned with the rostro-caudal axis. The length of the long axis of median dorsal opening varies from 3.7 to 4.2 mm, and the length of the short axis varies from 0.6 to 1.2 mm. The length of the long axis of median dorsal opening is about 5 times the length of the short axis. The distance between the anterior end of the median dorsal opening and the

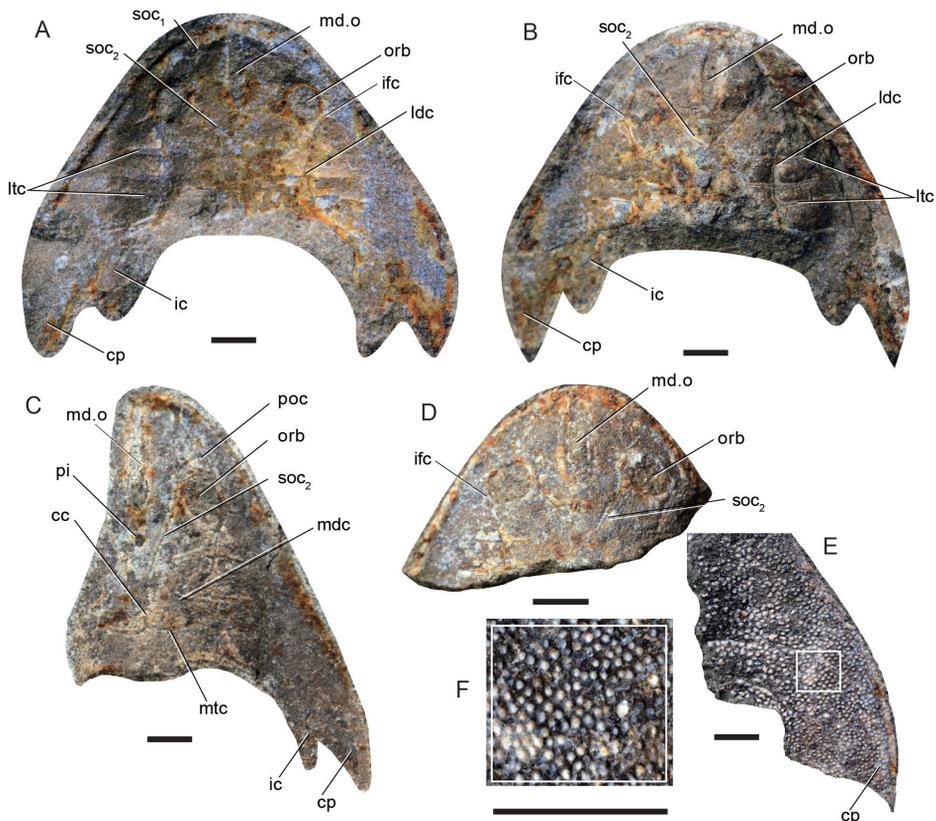


Fig. 3 Photographs of *Sinogaleaspis shankouensis* from the Silurian of Xiushui showing the morphology of the head-shield

A, B. external (A) and internal (B) moulds of a nearly complete head-shield, IVPP V 25135.1a, b; C. internal mould of an incomplete head-shield, V 25135.3; D. internal mould of an incomplete head-shield, V 25135.7b; E. internal mould of an incomplete head-shield, V 25135.11; F. close-up of granular tubercles (box region of Fig. 3E). soc₁, anterior supraorbital canal; other abbreviations see Fig. 2. Scale bars=2 mm

Table 1 Measurements of *Sinogaleaspis shankouensis*

(mm)

Items	Holotype	IVPP V 25135									
	GMC V 1751	.1	.2	.3	.4	.5	.6	.7	.8	.9	.10
Maximum length of the head-shield	17.1	16.9	15.9	17.2	17.3	18.4	17.4	–	–	17.9	15.5
Maximum width of the head-shield	–	20.4	20.8	20.6	19.3	17.8	20.3	–	20.6	19.7	17.2
Length of the head-shield in midline	11.5	9.6	10.6	12.7	10.8	–	10.8	–	10.7	10.6	9.7
Diameter of the orbital opening	2.1	2.1	1.9	2.0	1.8	2.0	1.6	2.1	2.2	1.9	1.5
Distance between the orbital openings	4.0	4.3	4.3	4.6	–	4.6	4.5	4.0	4.4	4.5	3.7
Long axis of the median dorsal opening	4.2	3.8	4.0	3.8	–	4.0	3.7	4.0	4.3	3.8	–
Short axis of the median dorsal opening	0.6	0.7	0.9	0.9	–	1.0	1.1	1.2	1.1	1.1	–
Length of the pre-pineal region in midline	6.2	5.4	5.7	6.6	–	6.7	5.8	6.4	5.4	5.6	–
Length of the post-pineal region in midline	5.3	4.2	4.9	6.1	–	–	5.0	–	5.3	5.0	–

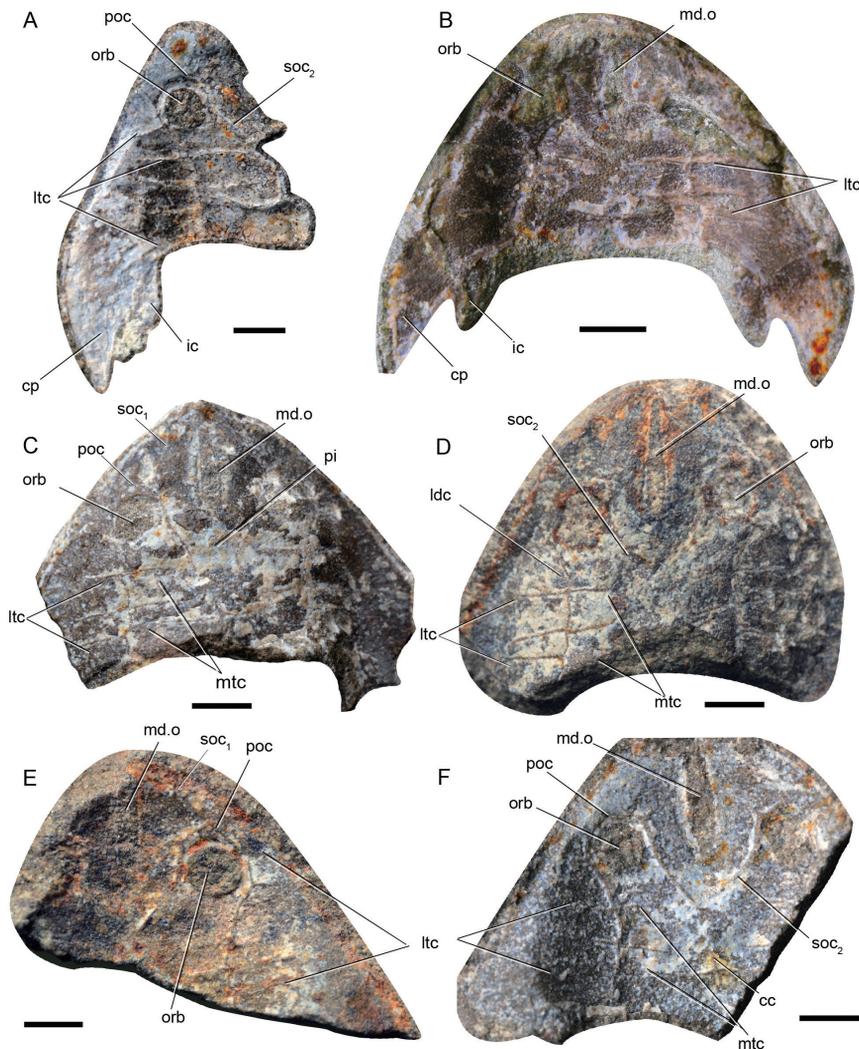


Fig. 4 Photographs of *Sinogaleaspis shankouensis* from the Silurian of Xiushui showing the sensory canal system

A. an incomplete external mould of the head-shield IVPP V 25135.4a; B. a complete external mould of the head-shield V 25135.9a; C. an incomplete internal mould of the head-shield V 25135.8; D. an incomplete internal mould of the head-shield V 25135.5; E. an incomplete external mould of the head-shield V 25135.7b; F. an incomplete external mould of the head-shield V 25135.2b. Abbreviations see Figs. 2, 3. Scale bars=2 mm

rostral margin of the head-shield is rather short (about 1 mm). The posterior end of the median dorsal opening extends posteriorly beyond the level of the center of the orbital opening, but in front of the level of the posterior margin of the orbital openings.

The orbital opening (orb, Figs. 2–6) has a dorsal position on the head-shield. The orbital opening is round in outline with a diameter ranging from 1.5 to 2.2 mm in 11 specimens (Table 1), roughly accounting for 1/5 of the length of the head-shield in midline. The distance between paired orbital openings is range from 3.7 to 4.6 mm in 11 specimens (Table 1).

The pineal opening is well preserved in specimen V 25135.3 (pi, Fig. 3C), which is located posterior to the level of the posterior margin of the orbital opening in the midline of the head-shield. The pineal opening is tiny and oval in outline with the length of the long axis about 0.54 mm, and the length of the short axis about 0.41 mm. Along the midline, the length of the pre-pineal region of head-shield ranges from 5.4 to 6.7 mm and the length of the post-pineal region ranges from 4.2 to 6.1 mm in 11 specimens (Table 1).

The sensory canal system of *S. shankouensis* is comprehensively reconstructed based on 10 specimens (Figs. 2–6). The well-preserved sensory canal system displays an eugaleaspid

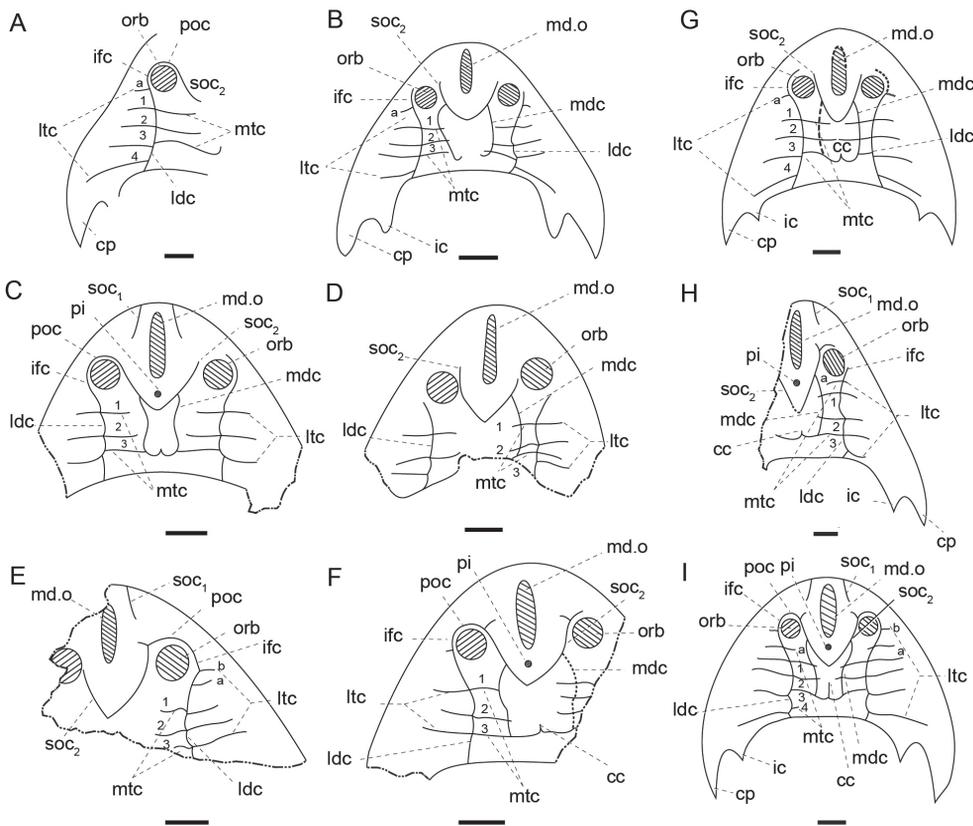


Fig. 5 Interpretative and synthetic drawings of the sensory canal system of *Sinogaleaspis shankouensis*
 A–F. interpretative drawings for Fig. 4; G, H. interpretative drawings for Fig. 3B, C; I. synthetic restoration
 Abbreviations: b. the second lateral transverse canal issuing from infraorbital canal;
 other abbreviations see Figs. 2, 3; scale bars=2 mm

pattern in distribution which consists of anterior supraorbital canals (soc_1), posterior supraorbital canals (soc_2), infraorbital canals (ifc), lateral dorsal canals (ldc), lateral transverse canals (ltc), median dorsal canals (mdc), preorbital commissure (poc), median transverse canals (mtc) and a short central canal (cc) (Figs. 2–6). The paired anterior supraorbital canals (soc_1 , Figs. 4C, E, 5C, E, H, I) slightly diverge posteriorly from the rostral margin, but do not connect with the posterior supraorbital canal (soc_2 , Figs. 2–6). The paired posterior supraorbital canals (soc_2 , Figs. 2–6) are V-shaped and converge posteriorly to the pineal opening.

The characterized median dorsal canal (mdc , Figs. 2–6) joins with the posterior supraorbital canal in about 45 degree angle at the level of the pineal opening, and posteriorly converges with the opposite one to form a U-shaped trajectory. A short previously unnamed longitudinal canal issuing from the middle of the U-shaped median dorsal canal, here, is termed as the central canal (cc , Figs. 2D, 3C, 4F, 5B, F, H, I). The infraorbital canals (ifc , Figs. 2–6) are positioned lateral to the orbital opening. Posteriorly, the infraorbital canal continues to extend as the lateral dorsal canal (ldc , Figs. 2–6), which is the main longitudinal canal on the head-shield. There are six pairs of lateral transverse canals (ltc , Figs. 2–6) and median transverse canals (mtc , Figs. 2–6) observed in our new specimens. In addition to four pairs of lateral transverse canals running from the lateral dorsal canal (ltc 1–4, Figs. 2, 5), two pair of additional lateral transverse canals (ltc a, b, Figs. 2, 5) are observed issuing from the infraorbital canals in specimen V 25135.7b (Figs. 4E, 5E). There are six pairs of median transverse canals (mtc , Figs. 2–6). In addition to the originally described 3 pairs of median transverse canals, three pairs of additional median transverse canals are observed in our new specimens. The most anterior pair of short transverse canals unite the infraorbital and posterior supraorbital canals in front of orbital openings, which probably represent the first median transverse canal, the preorbital commissure (poc , Figs. 2D, 3C, 4A, C, E, F, 5A, C, E, F, I, 7G–I).

The lateral margin of the head-shield is smooth and the exoskeleton of the head-shield is ornamented with closely set, tiny granular tubercles. The tubercles in the central part of the head-shield are bigger than those in the lateral part and the cornual process. There are about 10–15 tubercles per square millimeter in the center, whereas about 20–25 tubercles per square millimeter in the region of the cornual process (Fig. 3E, F).

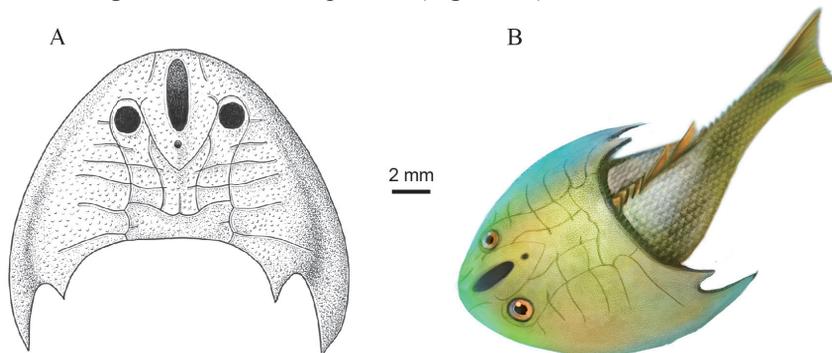


Fig. 6 Restoration of *Sinogaleaspis shankouensis*
A. dorsal view; B. anterior-lateral view

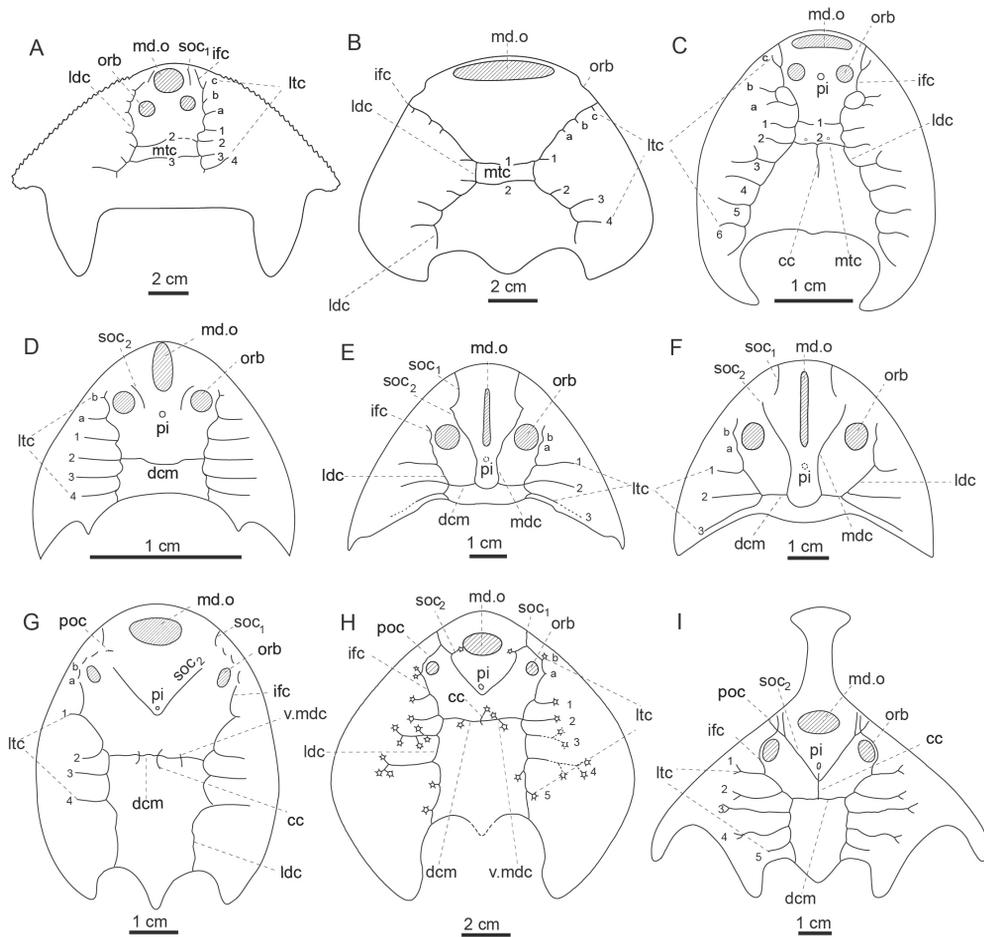


Fig. 7 The sensory canal systems of galeaspids in different groups

A–C. plesiomorphic taxa: A. *Dayongaspis hunanensis* (Pan and Zeng, 1985), B. *Hanyangaspis guodingshanensis* (P'an et al., 1975; Pan, 1986b), C. *Changxingaspis gui* (Wang, 1991); D–F. Eugaleaspiformes:

D. *Shuyu zhejiangensis* (Gai et al., 2011), E. *Eugaleaspis xujiaochongensis* (Liu, 1965), F. *E. changi* (Liu, 1975);

G, H. Polybranchiaspiformes: G. *Polybranchiaspis liaojiaoshanensis* (Liu, 1975), H. *Laxaspis qujingensis* (Liu, 1975);

I. Huananaspiformes: *Sanchaspis magalarostrata* (Pan and Wang, 1981)

Abbreviations: 1–6. the first to sixth lateral transverse canal or median transverse canal issuing from lateral

dorsal canal; a–c. the first to third lateral transverse canal issuing from the infraorbital canal;

dcm. dorsal commissure corresponding to the second median transverse canal;

v.mdc. vestige of median dorsal canal; other abbreviations see Figs. 2, 3

5 Discussion and conclusion

Sinogaleaspis shankouensis can be referred definitely to the Eugaleaspiformes by the longitudinal oval median dorsal opening and typical eugaleaspid-pattern sensory canal system (Zhu, 1992; Gai et al., 2005, 2018; Zhu and Gai, 2006). Gai et al. (2005) indicated that the three species assigned to *Sinogaleaspis* do not form a monophyletic group, but a paraphyletic group. The type species of *Sinogaleaspis*, *S. shankouensis* has a closer relationship to *Yunnanogaleaspis*

and higher eugaleaspids than to ‘*S.*’ *zhejiangensis* and ‘*S.*’ *xikengensis* (Gai et al., 2005), whereas ‘*S.*’ *zhejiangensis* is resolved as the deepest branching of the Eugaleaspiformes in later phylogenetic analyses (Fig. 8) (Zhu and Gai, 2006; Gai et al., 2018). Based on abundant new materials, especially the 3D preserved neurocrania, Gai et al. (2011) erected a new genus *Shuyu* for ‘*S.*’ *zhejiangensis*. By contrast, the nature of ‘*S.*’ *xikengensis* still needs more data for corroboration as the original description is mainly based on one poorly known specimen, especially its sensory canal system remains unknown. *Sinogaleaspis shankouensis* is similar to *Shuyu zhejiangensis*, *Meishanaspis lehmani*, and *Anjiaspis reticularis* from the Lower Silurian of Zhejiang Province in the subtriangular head-shield with spine-like cornual and inner cornual processes, but clearly different from them in the shape and position of median dorsal opening, the margin of head-shield, and pattern of sensory canals (Pan, 1986a; Wang, 1991; Gai and Zhu, 2005; Gai et al., 2011). The sensory canal system of *Sh. zhejiangensis* and *M. lehmani* are not of the typical eugaleaspid-pattern by being deficient of the median dorsal canal (Fig. 7D), probably representing a plesiomorphic condition of the Eugaleaspiformes (Gai et al., 2005, 2011).

By contrast, *S. shankouensis* exhibits a mélange of primitive and derived characters in the pattern of sensory canals. It possesses the U-shaped medial dorsal canal which is regarded as a derived character found in Eugaleaspiformes (mdc, Fig. 7E, F), V-shaped posterior supraorbital canals which is a derived character found in Polybranchiaspiformes and Huananaspiformes (soc₂, Fig. 7G–I), while it has more than one median transverse canals which is regarded as a primitive character found in plesiomorphic taxa such as Dayongaspididae, Hanyangaspididae and Xiushuiaspididae (mtc, Fig. 7A–C). In addition to four pairs of lateral transverse canals issuing from the lateral dorsal canal, the new materials of *S. shankouensis* also reveal two pairs of lateral transverse canals on infraorbital canals, a condition is strikingly similar to that of *Shuyu* and *Meishanaspis* (ltc a, b, Fig. 7D). Usually, there are 3–4 pairs of lateral transverse canals issuing from the infraorbital canal in the plesiomorphic taxa of galeaspids such as *Dayongaspis*, *Hanyangaspis*, and *Changxingaspis* (ltc a, b, c, Fig. 7A–C). Liu (1986) suggested that the number of lateral transverse canals has a decreasing tendency from six pairs to three pairs in Eugaleaspiformes. The vestiges of the lateral transverse canals can be observed on the infraorbital canals in some members of Eugaleaspiformes (e.g. *Eugaleaspis changi* and *E. xujiachongensis*) (ltc a, b, Fig. 7E, F) and Polybranchiaspiformes (e.g. *Polybranchiaspis liaojiaoshanensis* and *Laxaspis qujingensis*) (ltc a, b, Fig. 7G, H), which can be regarded as a corroborative evidence for this evolutionary tendency (Liu, 1986; Gai et al., 2005).

The most noteworthy feature of *S. shankouensis* and *A. reticularis* is the presence of much more than two pairs of median transverse canals (6 pairs in the former, 8 pairs in the latter), which is odd among about 80 described galeaspid species and has been questioned (Wang, 1991; Liu et al., 2014). In addition to the originally described 3 pairs of median transverse canals, additional three pairs of median transverse canals are observed in our new specimens of *S. shankouensis*. The six pairs of transverse canals (median transverse canals coupled with lateral transverse canals) form a grid distribution on the dorsal side of head-shield by intersecting with four longitudinal pairs (infraorbital canals, lateral dorsal canals, posterior

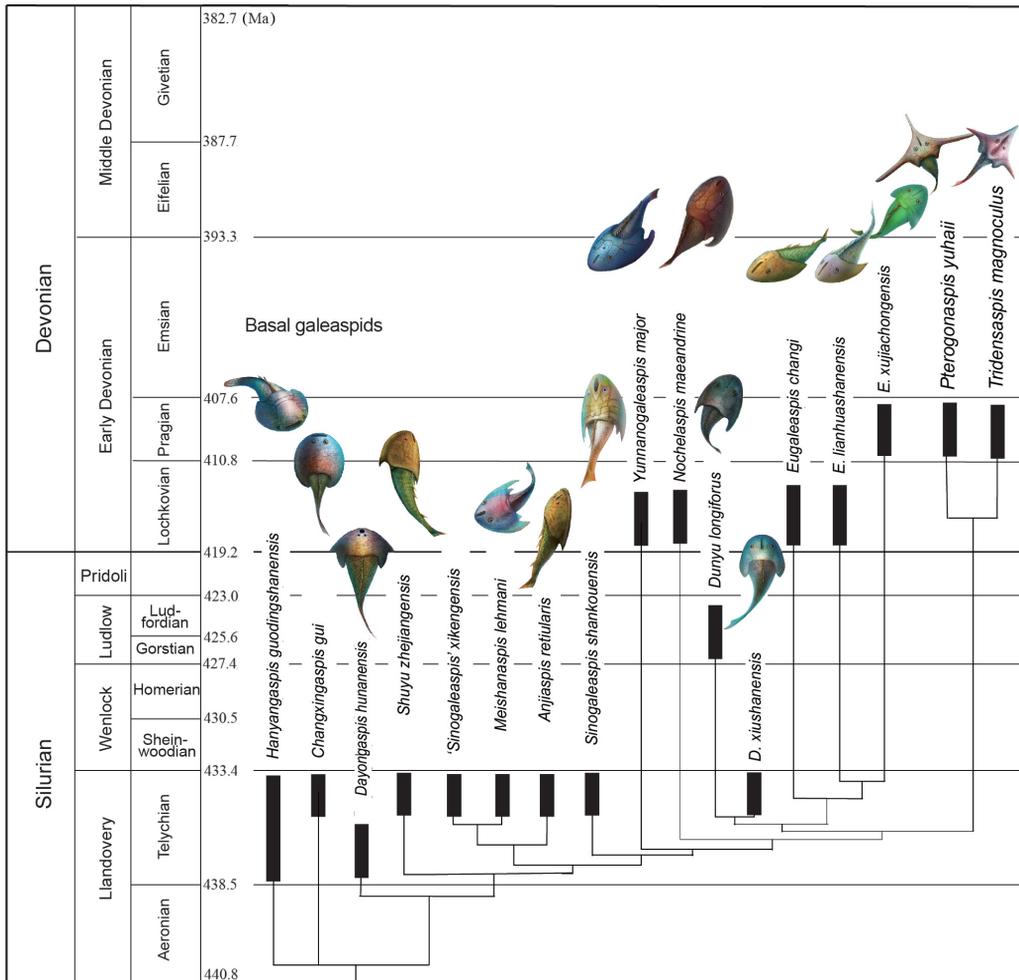


Fig. 8 Time-calibrated cladogram of the Eugaleaspiformes

Eugaleaspiformes experienced two diversifications in Silurian and Devonian (Solid columns represent known time ranges, thin lines represent 'ghost lineages') (modified from Zhu et al., 2012; Gai et al., 2018)

supraorbital canals, and median dorsal canals). The most anterior pair of median transverse canals, the preorbital commissures (poc) which link the infraorbital and posterior supraorbital canals in front of orbital openings, are also observed in some members of Polybranchiaspiformes and Huananaspiformes such as *Polybranchiaspis*, *Laxaspis* and *Sanchaspis* (poc, Fig. 7G–I). In addition, a short previously unnamed longitudinal canal of *S. shankouensis*, the central canal is also observed in *Changxingaspis*, *Polybranchiaspis*, *Laxaspis* and *Sanchaspis* (cc, Fig. 7C, G–I) issuing from the middle of dorsal commissure. In sum, the sensory canal system of *S. shankouensis* exhibits mosaic characters of plesiomorphic taxa, Eugaleaspiformes, Polybranchiaspiformes and Huananaspiformes, and probably represents plesiomorphic condition of vertebrates as Liu (1986) assumed.

The fossil-bearing strata of *S. shankouensis* also yield '*S.*' *xikengensis*, *Xiushuiaspis jiangxiensis*, and *X. ganbeiensis*, which are together named the *Sinogaleaspis-Xiushuiaspis* Fauna or the Maoshan Assemblage (P'an and Wang, 1983; Zhao and Zhu, 2010), because

similar galeaspid species including *Sh. zhejiangensis*, *M. lehmani*, *A. reticularis* and *C. gui* were found in the Maoshan Formation of Zhejiang Province (Pan, 1986a, 1988; Wang, 1991; Gai and Zhu, 2005; Gai et al., 2005). The *Sinogaleaspis-Xiushuiaspis* Fauna together with other plesiomorphic taxa of galeaspid (*Dayongaspis*, *Hanyangaspis*, *Kalpinolepis*, *Xiyuaspis*, and *Microphymaspis*) and the most primitive Polybranchiaspiforme (*Platylomaspis*) from the Silurian of the South China and Tarim probably represent the first diversification of galeaspid in the Telychian, Llandovery of the Silurian (Fig. 8), but they underwent a mass extinction during the Ludlow except for some Eugaleaspidiformes and Polybranchiaspiforme survived until the late Pragian of the Devonian (Zhu and Gai, 2006; Gai et al., 2018; Liu et al., 2019) (Fig. 8). The fish-bearing strata are referred to Silurian ‘upper red beds’ which reflect a nearshore, very shallow deltaic environment with the low nutrient, euphotic zone and rich oxidation (Rong et al., 2012). According to the evidence from the paleosalinity, and other geochemical data, Li (1996) thought that the sedimentary paleoenvironment of the Xikeng Formation at Xiushui, Jiangxi Province was suggestive of a brackish water body probably caused by a large deal of fresh water pouring into the sea from nearby rivers. In particular, most of specimens were collected from the Layer 13, which was composed of grey-green pelitic siltstone interbedded with a large deal of muddy gravels (Fig. 1B), strongly suggesting a short distance of potamic transportation. This indicates that the *Sinogaleaspis-Xiushuiaspis* Fauna may live in a fresh water environment in the river rather than their burial area in the sea.

Acknowledgements We are grateful to Zhao Ridong, Lin Xianghong, and Sun Baichuan for the great help in the field work, Guo Xiaocong, Yang Dinghua, and Huang Jinling for the illustrations and ecological restoration. This work was supported by Key Research Program of Frontier Sciences, CAS (QYZDB-SSW-DQC040, QYZDJ-SSW-DQC002), the National Natural Science Foundation of China (41572108, 41530102, 41972006), National Program for Support of Top-notch Young Professionals, and Strategic Priority Research Program of CAS (XDB26000000), State Key Laboratory of Palaeobiology and Stratigraphy (Nanjing Institute of Geology and Palaeontology, CAS, No. 193121) and Innovation Training Programs for Undergraduates, CAS.

江西志留纪山口中华盔甲鱼的再描述

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摘要: 基于对江西省修水县志留系西坑组发现的11个新标本的观察, 对存在争议的山口中华盔甲鱼(*Sinogaleaspis shankouensis*)进行了重新描述。深入的形态学研究表明, 山口中华

盔甲鱼的侧线感觉管系统展示出基于盔甲鱼类、真盔甲鱼目、多鳃鱼目和华南鱼目等多个类群的镶嵌特征。山口中华盔甲鱼的侧线感觉管系统由4条纵行干管和6条横向联络管相互交叉在头甲背面形成格栅状分布,可能反映了脊椎动物的祖先状态。山口中华盔甲鱼在动物群上属于中华盔甲鱼-修水鱼组合或茅山组合,该组合可能代表了盔甲鱼类在志留纪兰多维列世特里奇期的第一次适应辐射。江西修水西坑组古沉积环境指示了一种低盐度半咸水的近海环境,可能是由于大量淡水从附近河流涌入导致盐度降低,而含鱼层位灰绿色泥质粉砂岩中含有的大量泥砾则指示鱼化石经历了短距离的河流搬运。因此,该生物群可能生活在埋藏区域上游的淡水河流里。

关键词: 江西修水, 志留纪, 真盔甲鱼目, 中华盔甲鱼, 侧线感觉管系统

中图法分类号: Q915.861 文献标识码: A 文章编号: 1000-3118(2020)02-0085-15

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