

Original Articles

A New Species of *Jiangxialepis* (Galeaspida) from the Lower Telychian (Silurian) of Jiangxi and its Biostratigraphic Significance



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Abstract: A new species of Shuyuidae (Eugaleaspidiformes, Galeaspida), *Jiangxialepis jiujiangensis* sp. nov., is described from the lower Telychian (Llandovery, Silurian) Qingshui Formation in Jiujiang, Jiangxi Province, China. The new species differs from the type species *J. retrospectiva* from Wuhan, Hubei Province in its sharp and posteriorly positioned median dorsal spine and narrow spine-shaped inner cornual processes. The Silurian strata in Xiushui–Wuning area has provided a standard framework for the correlation of Silurian shallow marine red beds in South China. Thus, the finding of *J. jiujiangensis* from the Silurian Lower Red Beds (LRBs) in Jiangxi Province bears very important biostratigraphic significance. It can directly compare to *Jiangxialepis retrospectiva* from the Fentou Formation in Wuhan, Hubei Province in the genus level. This indicates that the age of the fish-bearing strata in Wuhan is most likely to be the early Telychian rather than middle Telychian as previously assumed.

Key words: Galeaspid, Qingshui Formation, Lower Red Beds, Silurian, Jiangxi Province

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1 Introduction

The Galeaspida is a jawless clade of stem-gnathostomes exclusively known from the Silurian and Devonian of South China, Tarim, and North China blocks (Zhu et al., 1994; Janvier, 1996; Zhu and Gai, 2006; Janvier et al., 2009; Sansom 2009; Gai et al., 2018), which is important for us understanding the origin of major clades of jawed vertebrates (Xiao, 2022). Geleaspid is of great significance in Siluro–Devonian regional stratigraphic issues, especially in the correlation of Silurian shallow marine red beds in South China and Tarim because they underwent a rapid radiation in these regions with abundant fossil records (Zhao, 2005; Zhao et al., 2009, 2014, 2018; Shan et al., 2022a, b). Among galeaspid, Shuyuidae, the most primitive Eugaleaspidiformes that sister to all other Eugaleaspidiformes, provides important fossil evidence in the correlation of Silurian Lower Red Beds (LRBs) in South China (Shan et al., 2022a, b). The Shuyuidae is assumed to be diversified from the plesiomorphic clades of galeaspid no later than the early Telychian (Llandovery), because their oldest fossil records are all from the Silurian Lower Red Beds, i.e., *Shuyu* and *Meishanaspis* from the Tangchiawu Formation in Northwest Zhejiang (Pan, 1986; Gai et al., 2005, 2011; Shan et al., 2022a); *Qingshuia* from the Qingshui Formation in Northwest Jiangxi (Shan et al., 2022a).

Liu et al. (2021a) reported *Jiangxialepis retrospectiva* from the upper part of the Fentou Formation at Huangjintang, Wuhan, Hubei Province, which was considered to be the only fossil record of Shuyuidae occurring in the middle Telychian. For a long time, all Silurian fish-bearing strata including the *Jiangxialepis*-bearing strata in Wuhan were roughly grouped into the Fentou Formation (equivalent to the Guodingshan Formation in Pan et al., 1975 and Li, 1980), as the Silurian strata exposed in Wuhan has long been considered to contain exclusively the Fentou Formation (BGMHRP, 1990; Chen and Jin, 1996; Zong et al., 2011, 2017). Recently, however, a new horizon of Silurian marine red beds containing abundant galeaspid and chondrichthyans has been discovered underlying the Fentou Formation in Wuhan. Therefore, the precise horizon and age of the fossil fishes including *Jiangxialepis* in Wuhan deserve further investigation. Here we describe a new species of *Jiangxialepis* from the Qingshui Formation of early Telychian age in Jiujiang, Jiangxi Province, China. It not only increases our knowledge of Silurian galeaspid diversity, but also provide reliable fossil evidence for clarifying the ambiguous horizon and age of the *Jiangxialepis* in Wuhan, Hubei Province.

2 Geological Setting

The specimens of *Jiangxialepis jiujiangensis* sp. nov. were collected from the upper part of the Qingshui

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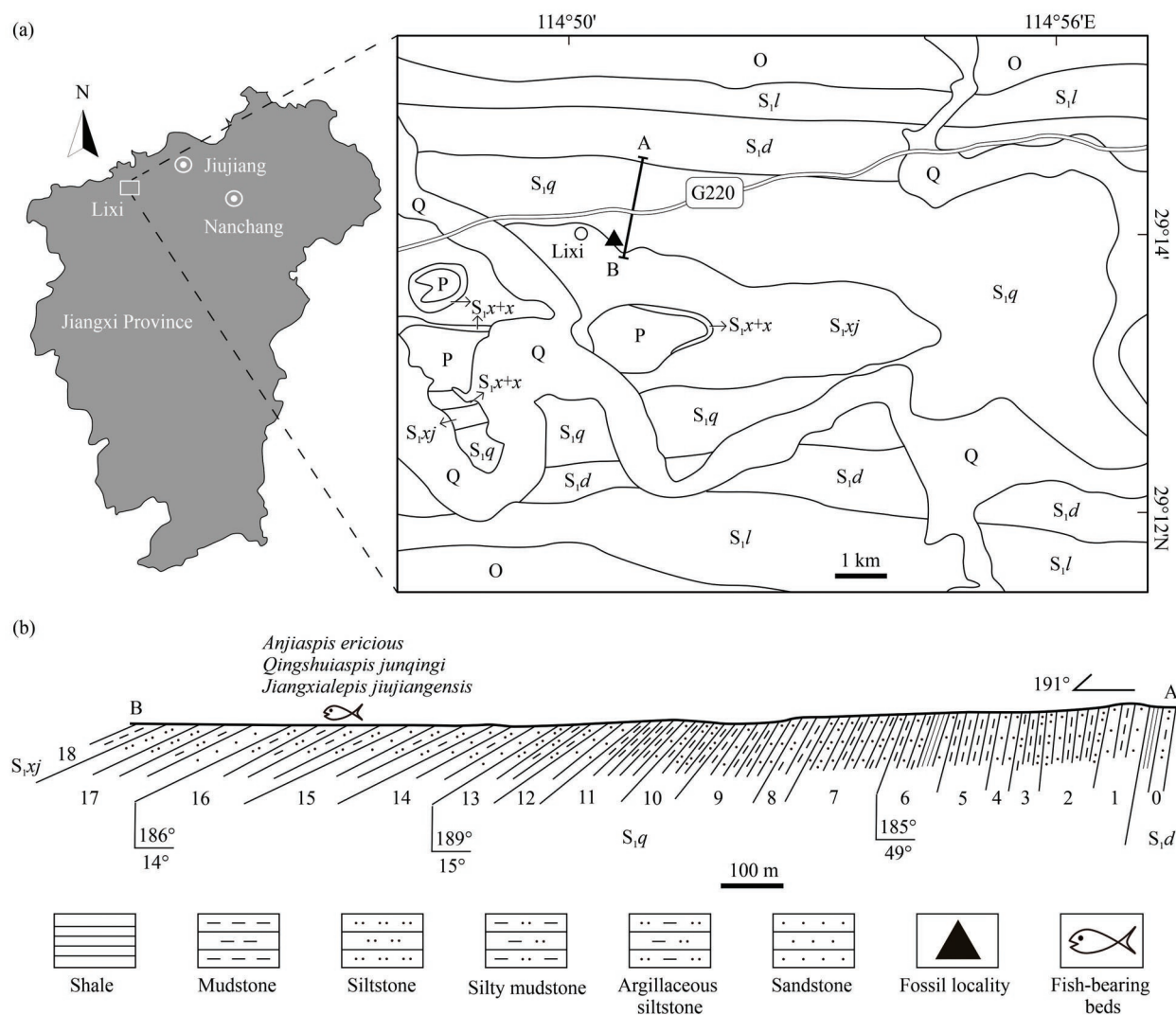


Fig. 1. Geological setting of *Jiangxialepis jiujiangensis* sp. nov..

(a) Regional geological map at the fossil locality near Lixi, Jiujiang, Jiangxi Province, China (modified after Chen and Rong, 1996); (b) geological section of the fish-bearing Qingshui Formation. Abbreviations: O–Ordovician; P–Permian; Q–Quaternary; S_{1l}–Lishuwo Formation; S_{1d}–Dianbei Formation; S_{1q}–Qingshui Formation; S_{1xj}–Xiajiaqiao Formation; S_{1x+x}–Xikeng Formation plus Xiaoxi Formation.

Formation at Lixi Town, Wuning County, Jiujiang City, Jiangxi Province, China (Fig. 1a). The Silurian marine strata in this area can be subdivided into the Lishuwo, Dianbei, Qingshui, Xiajiaqiao, Xikeng, and Xiaoxi formations in ascending chronological order (Zhao and Zhu, 2010; Wang et al., 2018, 2021; Rong et al., 2019). The fish-bearing Qingshui Formation is mainly comprised of purple-red and yellow-green sandstones, siltstones, argillaceous siltstones, silty mudstones, and mudstones (Fig. 1b), being known as the Silurian Lower Red Beds (LRBs) in South China (Rong et al., 1990, 2019; Chen and Rong, 1996; Shan et al., 2022a). The formation has yielded diversified vertebrate remains including galeaspid *Qingshuiaspis junqingi*, *Anjiaspis ericius*, and some undescribed species of Dayongaspididae, Xiushuiaspididae, and Gumuaspididae; and chondrichthyans *Neosinacanthus* (Shan et al., 2022a, b). The early vertebrate assemblage in the Qingshui

Formation is referred to as the Wentang Assemblage (Zhao and Zhu, 2010, 2014; Shan et al., 2022b) which is also known in other LRBs in South China, i.e., The Rongxi Formation in Northwest Hunan and Southeast Chongqing, the Houjiatang Formation in East Anhui and South Jiangsu, the Tangchiawu Formation in Northwest Zhejiang and Southeast Anhui. The Wentang Assemblage is comparable to the Tataertag Assemblage found in the Tataertag Formation in Northwest Tarim Basin (Zhao, 2005; Zhao et al., 2009, 2014; Shan et al., 2022b). Although the precise age of the Qingshui Formation is difficult to determine, an age of the early Telychian is proposed based on the evidence of the middle Telychian Xiushan Fauna from the overlying Xiajiaqiao Formation (Shan et al., 2022a).

The Qingshui Formation at the fossil locality near the Lixi Town has been measured (Fig. 1b) and its lithological description is provided as follows:

Xiajiaqiao Formation (S₁xj)

18. Yellow-green thin mudstones 10 m

Conformity

Qingshui Formation (S₁q) 796.9 m

17. The lower part consists of gray-yellow and yellow-green medium to thick sandstones intercalated with purple-red thin argillaceous siltstones, and the upper part consists of purple-red thin to medium siltstones. 50.8 m

16. Purple-red and yellow-green thin argillaceous siltstones intercalated with purple-red thin silty, mudstones, yielding galeaspids *Anjiaspis ericius*, *Qingshuiaspis junqingi*, and *Jiangxialepis jiujiangensis* sp. nov.. 39.7 m

15. The lower part consists of purple-red thin siltstones intercalated with purple-red thin argillaceous siltstones and gray mudstones, containing purple-red muddy gravels, and the upper part consists of gray-green and yellow-green medium to thick sandstones intercalated with purple-red thin argillaceous siltstones and silty mudstones. 28.4 m

14. The lower part consists of purple-red thin to medium argillaceous siltstones intercalated with gray-green thin to medium sandstones, and the upper part consists of thin argillaceous siltstones intercalated with gray-yellow thin sandstones. 40.3 m

13. Purple-red thin argillaceous siltstones intercalated with purple-red thin silty mudstones. 32.5 m

12. Yellow-green medium to thick sandstones intercalated with gray-green thin siltstones. 24.8 m

11. Gray-green thick sandstones and purple-red thin mudstones. 49.0 m

10. Purple-red thin silty mudstones and argillaceous siltstones. 37.8 m

9. Gray-yellow and gray-green thin to thick sandstones interbedded with purple-red thin mudstones. 53.8 m

8. Purple-red thin mudstones, silty mudstones intercalated with purple-red thin to medium siltstones. 35.6 m

7. Gray-yellow and gray-green medium and thick sandstones intercalated with purple-red thin silty mudstones. 74.6 m

6. Purple-red thin mudstones, gray-yellow thin to medium sandstones intercalated with purple-red shales. 77.8 m

5. Purple-red thin mudstones intercalated with thin silty mudstones. 19.7 m

4. Purple-red thin mudstones intercalated with dark-gray medium sandstones. 24.7 m

3. Purple-red thin mudstones and argillaceous siltstones intercalated with thin silty mudstones. 41.4 m

2. The lower part consists of gray thin to medium siltstones, purple mudstones intercalated with thin to medium sandstones, the upper part consists of gray-green thin to medium sandstones intercalated with purple-red thin siltstones. 104.7 m

1. The lower part consists of yellow-green thick sandstones and purple-red mudstones, and the upper part consists of yellow-green and gray thin to medium sandstones. 61.3 m

Conformity

Dianbei Formation (S₁d)

0. Yellow-green shales intercalated with thin argillaceous siltstones. >20.0 m

3 Samples and Methods

The materials of *Jiangxialepis jiujiangensis* sp. nov. include two nearly complete headshields (IVPP V 30955.1–2) and 13 incomplete headshields (IVPP V 30955.3–15). All these specimens are permanently housed and accessible for examination in the collection of the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Chinese Academy of Sciences (CAS). The fossils were prepared mechanically using a vibro tool with a tungsten-carbide bit or a needle. All specimens were studied under an Olympus SZ61 zoom stereo microscope and measured with a digital vernier calliper. All photographs were captured using a Canon EOS 5D Mark

III camera coupled with a Canon macro photo lens EF 100 mm 1: 2.8L for the general morphology, and with a Canon macrophoto lens MP-E 65 mm 1: 2.8 1–5× for a close-up of the ornamentation.

4 Systematic PaleontologySubclass **Galeaspida** Tarlo, 1967Order **Eugaleaspiformes** (Liu, 1965) Liu, 1980Family **Shuyuidae** Shan, Zhu, Zhao, Pan, Wang and Gai, 2020Genus ***Jiangxialepis*** Liu, Huang, Zong and Gong, 2021**Type species:** *Jiangxialepis retrospina* Liu, Huang, Zong and Gong, 2021.

Diagnosis (emended): A small-sized eugaleaspid fish with subtriangular headshield; width slightly greater than length; posterior margin of the headshield protruding posteriorly to form a median dorsal spine; corneal process spine-shaped, projecting caudo-laterally; inner corneal process shorter than the corneal process, spine-shaped or narrow leaf-shaped, projecting caudo-laterally; median dorsal opening longitudinal oval in outline with its anterior end obviously disrupting the rostral margin of the headshield; orbital openings dorsally positioned, large and oval; pineal opening small, level with the center of orbital openings; sensory canal system consisting of funnel-shaped posterior supraorbital canals, infraorbital canals, lateral dorsal canals, 7 pairs of lateral transverse canals, and one dorsal commissure; lateral margin of the headshield smooth; ornamentation composed of coarse granular tubercles.

Remarks: The emended *Jiangxialepis* includes two species, *J. retrospina* and *J. jiujiangensis* sp. nov., with synapomorphies including an unclosed rostral margin and a median dorsal spine of the headshield. Previous phylogenetic analysis indicates that *Jiangxialepis*, *Qingshuiaspis*, *Shuyu*, and *Meishanensis* form a monophyletic group, the family Shuyuidae (Shan et al. 2022a). *Jiangxialepis* differs from the other members of Shuyuidae in its unclosed rostral margin of the headshield. It further differs from *Shuyu* and *Meishanaspis* in possessing a median dorsal spine on the dorsal side of the headshield. *Shuyu* is resolved as the sister to all other members of Shuyuidae (Shan et al. 2022a), which indicates that the unclosed rostral margin of *Jiangxialepis* is a derived character for the family. Therefore, the unclosed rostral margin of the headshield, previously considered to be an autapomorphy of *Rumporostralis* of Sinogaleaspidae, has evolved independently at least twice among Eugaleaspiformes.

Jiangxialepis jiujiangensis Shan, Zhao and Gai sp. nov.**Etymology:** *Jiujiang*, after the Jiujiang City in Jiangxi Province, China, where the fossil site located.**Holotype:** a nearly complete headshield, IVPP V 30955.2 (Fig. 2b).**Referred specimens:** a nearly complete headshield, IVPP V 30955.1 (Fig. 2a), and 13 incomplete headshields, IVPP V 30955.3–15 (Figs. 2c–e, g, 3a–d, 4a–e).**Type locality and horizon:** Lixi Town, Wuning County, Jiujiang City, Jiangxi Province, China; Qingshui Formation, lower Telychian, Llandovery, Silurian.

Differential diagnosis: *Jiangxialepis jiujiangensis* differs from the type species *J. retrospina* in the shape of the median dorsal spine and the inner corneal processes, and their relative position. The median dorsal spine of *J. jiujiangensis* is longer and much sharper than that of *J. retrospina*, and its posterior end levels with the ends of the corneal processes, while the posterior end of *J. retrospina* is anterior to the ends of the corneal processes (Fig. 5). In

addition, the inner corneal processes of *J. jiujiangensis* are narrow and spine-shaped, while those of *J. retrospina* are relatively broad and leaf-shaped (Fig. 5).

Measurements: See Table 1.

Description: *Jiangxialepis jiujiangensis* is a small-sized jawless fish with a subtriangular headshield that arches dorsally along the midline (Fig. 2a–d). The measurements of 7 specimens of *J. jiujiangensis* show that

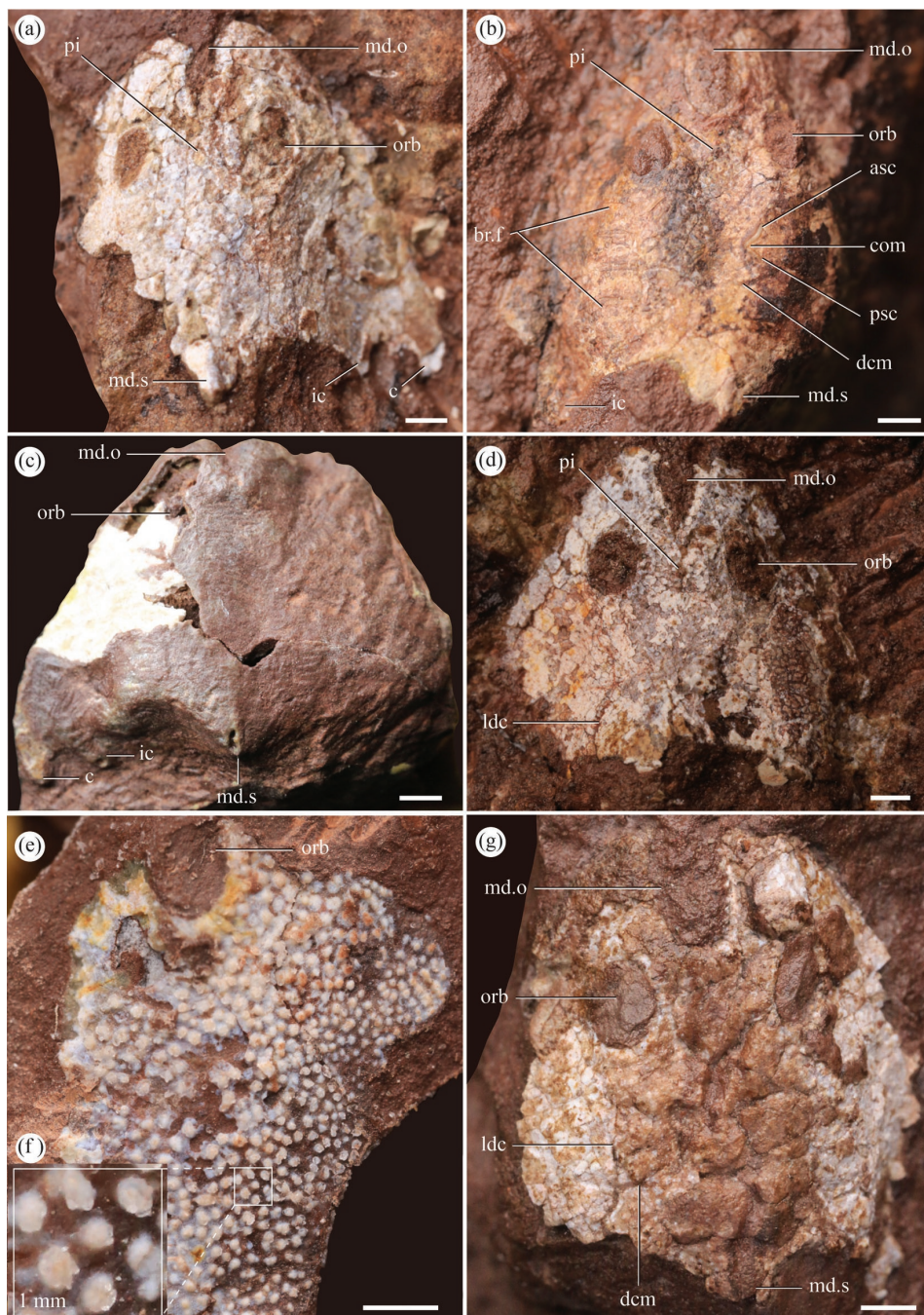


Fig. 2. Photographs of *Jiangxialepis jiujiangensis* sp. nov. in dorsal view.

(a) A nearly complete internal mould of the headshield, IVPP V 30955.1; (b) a nearly complete internal mould of the headshield, holotype, V 30955.2; (c) an incomplete internal mould of the headshield, V 30955.3; (d) an incomplete internal mould of the headshield, V 30955.4; (e) an incomplete external mould of the headshield, V 30955.5; (f) close-up of granular tubercles (box region of Fig. 2e); (g) an incomplete internal mould of the headshield, V 30955.6. Abbreviations: asc—anterior semicircular canal; br.f—branchial fenestra; c—cornual process; com—commissural division of two vertical semicircular canals; dcm—dorsal commissure; ic—inner cornual process; ldc—lateral dorsal canal; md.o—median dorsal opening; md.s—median dorsal spine; orb—orbital opening; pi—pineal opening; psc—posterior semicircular canal. Scale bars = 2 mm.

the headshield has a little size variation with its maximum length varying from 16.7 to 18.6 mm and its maximum width varying from 22.0 to 22.8 mm. Caudally, the headshield protrudes into a pair of cornual and inner cornual processes. The cornual processes are spine-like, short, projecting caudo-laterally and rapidly tapered off (c; Figs. 2a, c, 4a, c, d). The distance between paired cornual processes is about 20.0 mm (Table 1). The inner cornual processes are spine-like, caudo-laterally oriented, a little shorter than the cornual processes (ic; Figs. 2a–c, 4a, d). The distance between paired inner cornual process is about 14.4 mm (Table 1). Between paired inner cornual processes, the posterior margin of the headshield protrudes posteriorly to form a median dorsal spine (md.s; Figs. 2a–c, g, 4a). The median dorsal spine is triangular in shape with a sharp end, extending along the midline for about 5 mm. The posterior end of median dorsal spine levels approximately with the posterior ends of cornual processes.

The median dorsal opening (md.o; Figs. 2a–d, g, 3a, d, 4a, b) is located in the anterior part of the headshield, displaying a slender longitudinal oval shape as in other eugaleaspiiforms. The length of the long axis of median dorsal opening ranges from 4.4 to 4.8 mm, and the length of the short axis of that ranges from 2.0 to 2.3 mm (Table 1). The long axis is about 2.2 times the short axis in length. The posterior end of median dorsal opening is positioned anterior to the level of anterior margin of orbital openings. The anterior end of median dorsal opening extends to and disrupts the rostral margin of the headshield, which implies the median dorsal opening may partly open to the ventral side of the headshield.

The orbital opening (orb; Figs. 2a–g, 3a, d, 4a, b) is oval in outline, dorsally positioned, and not close to the midline

of the headshield with the interorbital distance varying from 4.0 to 4.7 mm. The length of the long axis of orbital opening ranges from 3.0 to 3.3 mm, and the length of the short axis of that ranges from 1.9 to 2.3 mm (Table 1).

The pineal opening (pi; Figs. 2a, b, d, 4a) is located at the level of the centers of two orbital openings in the midline of the headshield. The pineal opening is tiny and round in outline with a diameter about 0.6 mm (Table 1). Along the midline of the headshield, the length of pre-pineal region is about 6.0 mm, and the length of post-pineal region is about 12.0 mm. The post-pineal region is nearly 2 times the pre-pineal region in length.

The sensory canal system of *J. jiujiangensis* is comprehensively reconstructed mainly based on 4 specimens (IVPP V 30955.7–10; Fig. 3a–d). It displays the same distribution pattern as that of *J. retrospina* which consists of a pair of posterior supraorbital canals (soc₂), a pair of infraorbital canals (ifc), a pair of lateral dorsal canals (ldc), seven pairs of lateral transverse canals (ltc), and a dorsal commissure (dcm). Paired posterior supraorbital canals (soc₂; Fig. 3a) are funnel-shaped and mesial to the orbital opening, being isolated and unconnected with other sensory canals. Paired infraorbital canals (ifc; Fig. 3e, f, h) issue anterolateral to the orbital opening and extend posteriorly along the lateral side of the orbital opening. Posteriorly, a pair of infraorbital canals join smoothly with the lateral dorsal canals (ldc; Figs. 2d, g, 3e–h) to form the main longitudinal canal of the sensory canal system. The lateral dorsal canals extend to the posterior end of the headshield and may connect with the main lateral line sensory canals on the body. Seven pairs of lateral transverse canals issue from the main longitudinal canal and are spaced with equal intervals. The anterior three pairs of lateral transverse canals (ltc_{a–c}; Fig. 3e–h) emerge from the infraorbital canals, while the posterior four pairs of lateral transverse canals (ltc_{1–4}; Fig. 3e–h) from the lateral dorsal canal. Paired lateral dorsal canals are connected by a dorsal commissure (dcm; Figs. 2b, g, 3e–h) which is approximately level with the second lateral transverse canal (ltc₂).

The lateral margin of the headshield is smooth and the exoskeleton of the headshield is ornamented with coarse, sparse granular tubercles. The tubercles around orbital openings are bigger than those in the lateral part of the headshield, with about 3–4 tubercles per square millimeter around orbital openings, whereas about 7–8 tubercles per square millimeter in the region away from orbital openings (Fig. 2e, f).

The ventral side of the headshield can be observed in several incompletely preserved specimens (IVPP V 30955.11–15; Fig. 4a–e), which shows a large dome oralobranchial chamber (Fig. 4a, b) encompassed by a pair of ventral rims (vr; Fig. 4a–e) and the dorsal part of the headshield. The ventral rim is narrow at the anterolateral region of the headshield, broadens gradually at the posterior region, and protrudes posterolaterally to form the base of cornual and inner cornual processes. In the specimen IVPP V 30955.12 (Fig. 4b), several depressions along the mesial side of ventral rim may display the position of branchial fenestra (br.f; Figs. 2b, 4b). The oralobranchial chamber opens outside by a large pear-

Table 1 Measurements of *Jiangxialepis jiujiangensis* sp. nov. (mm)

Items	IVPP V 30955						
	.1	.2	.3	.4	.6	.7	.11
Maximum length of the headshield	18.5	18.6	16.7	–	17.8	–	17.7
Maximum width of the headshield	22.6	22.4	22.8	–	–	–	22.0
Length of the head-shield in midline	18.5	18.6	16.5	–	17.8	–	17.7
Long axis of the orbital openings	3.1	3.0	–	3.2	3.2	3.1	3.3
Short axis of the orbital openings	1.9	1.9	–	2.2	2.3	2.1	2.2
Distance between the orbital openings	4.7	4.3	–	4.2	4.2	4.7	4.0
Long axis of the median dorsal opening	4.5	4.7	–	4.4	4.5	4.8	4.5
Short axis of the median dorsal opening	–	2.3	–	2.0	2.2	2.2	2.2
Diameter of the pineal opening	0.6	0.5	–	–	–	0.6	–
Length of the pre-pineal region	6.0	5.8	–	6.0	–	6.2	–
Length of the post-pineal region	11.6	12.2	–	–	–	–	–
Distance between paired cornual processes	20.4	–	19.2	–	–	–	19.0
Distance between paired inner cornual process	14.4	15.6	–	–	–	–	12.8

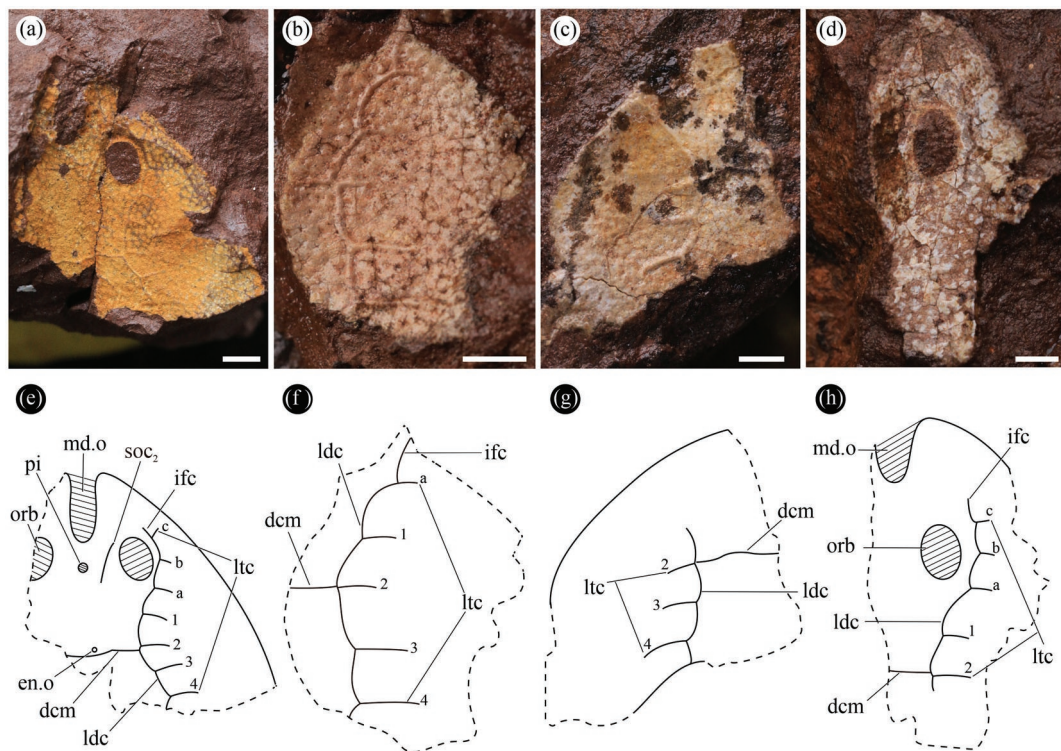


Fig. 3. Photographs and interpretative drawings of *Jiangxialepis jiujiangensis* sp. nov.. (a–d) Four incomplete external moulds of the headshields, IVPP V 30955.7 (a), V 30955.8 (b), V 30955.9 (c), V 30955.10 (d); (e–h) interpretative drawings of a–d, respectively. Abbreviations see Fig. 2 plus 1–4, the first to fourth lateral transverse canal issuing from lateral dorsal canal; a–c, the first to third lateral transverse canal issuing from infraorbital canal; en.o–endolymphatic opening; ifc–infraorbital canal; ltc–lateral transverse canal; soc2–posterior supraorbital canal. Scale bars = 2 mm.

shaped oralobranchial fenestra, which probably is covered by a large ventral plate, although it is not preserved in all specimens.

In the holotype (IVPP V 30955.2; Fig. 2b), anterior to the dorsal commissure, a pair of incompletely preserved natural casts of the labyrinth cavity reveal partial morphology of the inner ear. Two vertical semi-circular canals constitute distinct loops (asc, psc; Fig. 2b), and meet medially to form a vertical tube for the crus commissure (com; Fig. 2b). In specimen IVPP V 30955.7 (Fig. 3a), a small round opening probably for the external opening of endolymphatic duct (en.o; Fig. 3a) can be observed anterior to the dorsal commissure.

5 Discussion

During Early Palaeozoic Era, geleaspids have experienced several rapid radiations in South China and Tarim with abundant fossil records (Zhao, 2005; Zhao et al., 2009, 2014, 2018; Shan et al., 2022a, b). Therefore, they played an important role in correlating the Siluro-Devonian regional stratigraphy. The finding of *Jiangxialepis jiujiangensis* from the upper part of the Qingshui Formation in Jiangxi Province bears very important biostratigraphic significance. The Silurian marine strata are widespread in Xiushui–Wuning area of Jiangxi Province and can be subdivided into the Lishuwo, Dianbei, Qingshui, Xiajiaqiao, Xikeng, and Xiaoxi formations in ascending chronological order (Zhao and Zhu, 2010; Wang

et al., 2018, 2021; Rong et al., 2019). The Qingshui Formation and the Xikeng Formation are known as the Silurian Lower Red Beds (LRBs) and Upper Red Beds (URBs) respectively, which clip the Xiajiaqiao Formation in between. Recent biostratigraphic studies suggest that the Qingshui Formation (LRBs) is characterized by the occurrence of Shuyuidae, whereas the Xikeng Formation (URBs) by the occurrence of Sinogaleaspidae (Shan et al., 2020, 2022a). As the ages of the Qingshui Formation (LRBs) and the Xikeng Formation (URBs) can be well constrained by the sandwiched Xiajiaqiao Formation which yields the Xiushan Fauna. Therefore, the Silurian strata in Xiushui–Wuning area can provide a standard framework for the division and correlation of Silurian shallow marine red beds in South China (Zhao and Zhu, 2014; Shan et al., 2022a). For example, the findings of *Qingshuiaaspis* and *Anjiaspis* in the Qingshui Formation suggest that the fish assemblage consisting of *Shuyu*, *Meishanaspis*, and *Anjiaspis* from the Silurian marine red beds in Northwest Zhejiang is more comparable to that of the Qingshui Formation (LRBs) than that of the Xikeng Formation (URBs). Therefore, the age of fish-bearing marine red beds in northwestern Zhejiang has been modified as early Telychian, about 438 million years ago (Shan et al., 2022a).

Here, we further show that the finding of *Jiangxialepis jiujiangensis* sp. nov. in the Qingshui Formation can directly compare to *Jiangxialepis retrospina* from the Fentou Formation in Wuhan, Hubei Province in the genus level. *J. jiujiangensis* is strikingly resembling the type species *J.*

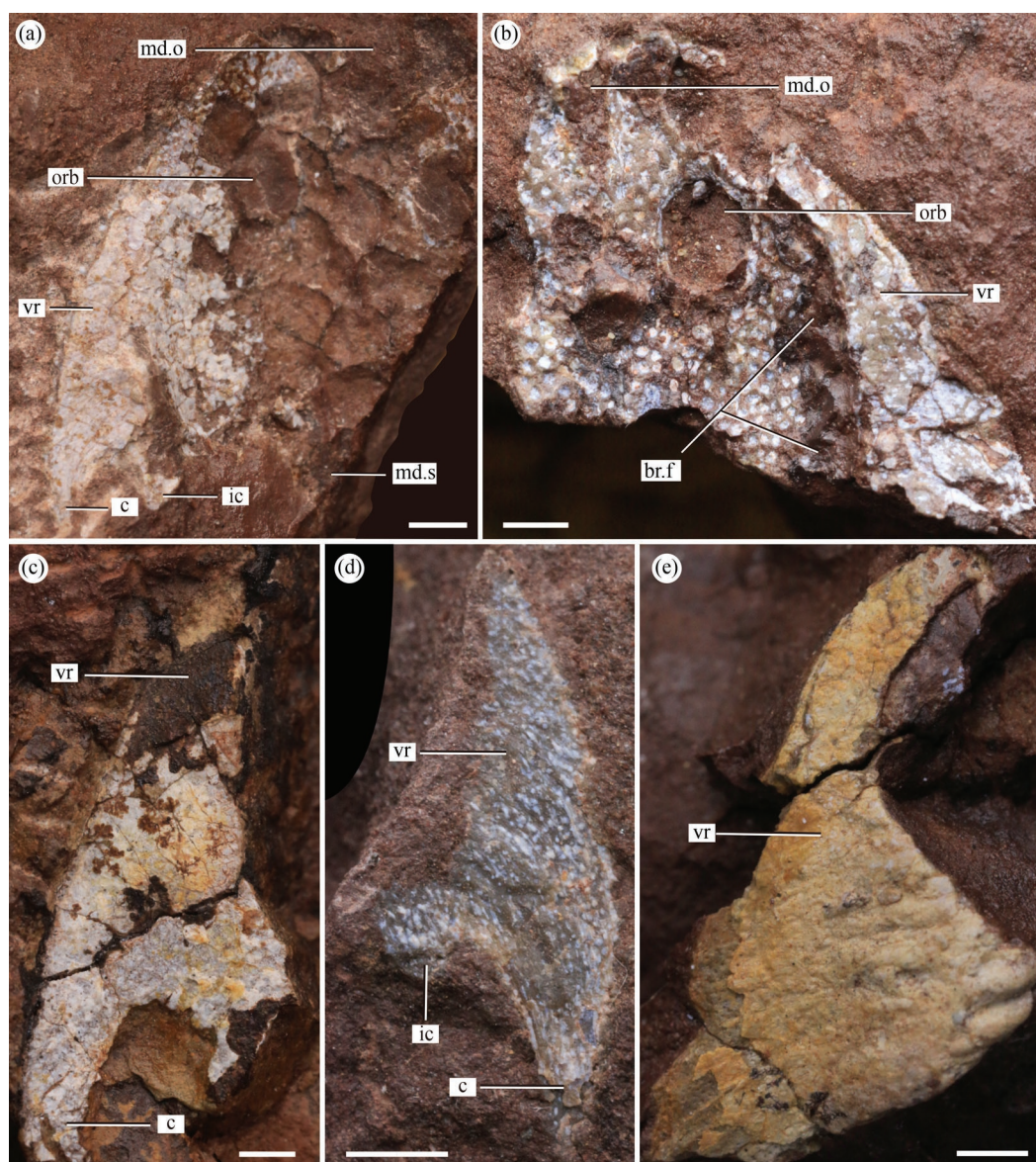


Fig. 4. Photographs of *Jiangxialepis jiujiangensis* sp. nov..

(a) An incomplete internal mould of the headshield, IVPP V 30955.11; (b) an incomplete external mould of the headshield, V 30955.12; (c) an incomplete internal mould of the headshield, V 30955.13; (d) an incomplete internal mould of the headshield, V 30955.14; (e) an incomplete internal mould of the headshield, V 30955.15. Abbreviations see Fig. 2 plus vr—ventral rim. Scale bars = 2 mm.

retrospina in bearing an unclosed rostral margin and a median dorsal spine of the headshield. However, it differs from *J. retrospina* in its sharp and posteriorly positioned median dorsal spine and narrower spine-shaped inner cornual processes. Therefore, a new species of *Jiangxialepis* can be erected. The occurrence of the new species of *Jiangxialepis* in LRBs of Jiangxi Province suggested that the age of the fish-bearing strata in Wuhan is most likely to be the early Telychian rather than middle Telychian as previously assumed.

The Silurian strata exposed in Wuhan has long been considered to contain exclusively the Fentou Formation (equivalent to the Guodingshan Formation in Pan et al., 1975 and Li, 1980) (BGMRHP, 1990; Chen and Jin, 1996; Zong et al., 2011, 2017). Because of that, the fish fossils

from the Silurian in Wuhan include galeaspids *Hanyangaspis guodingshanensis*, *Jiangxialepis retrospina*; and chondrichthyans *Sinacanthus wuchangensis*, *S. fancunensis*, *S. tringulatus*, and *Neosinacanthus planispinatus*, were all roughly grouped into the Fentou Formation (Pan et al., 1975; Li, 1980; Zong et al., 2011, 2017; Liu et al., 2021a). These fish fossils have been referred to as the *Hanyangaspis-Sinacanthus* assemblage (Zhu and Wang, 2000) or the Fentou Assemblage (Zhao and Zhu, 2010, 2014). The Fentou Formation in Wuhan yields characteristic invertebrate fauna represented by trilobites *Coronocephalus*, *Kailia*, brachiopods *Striispirifer*, and bivalves *Orthonota*, which is comparable to the *Salopinella-Coronocephalus-Sichuanoceras* fauna or the Xiushan Fauna from the Xiushan and Xiajiaoqiao

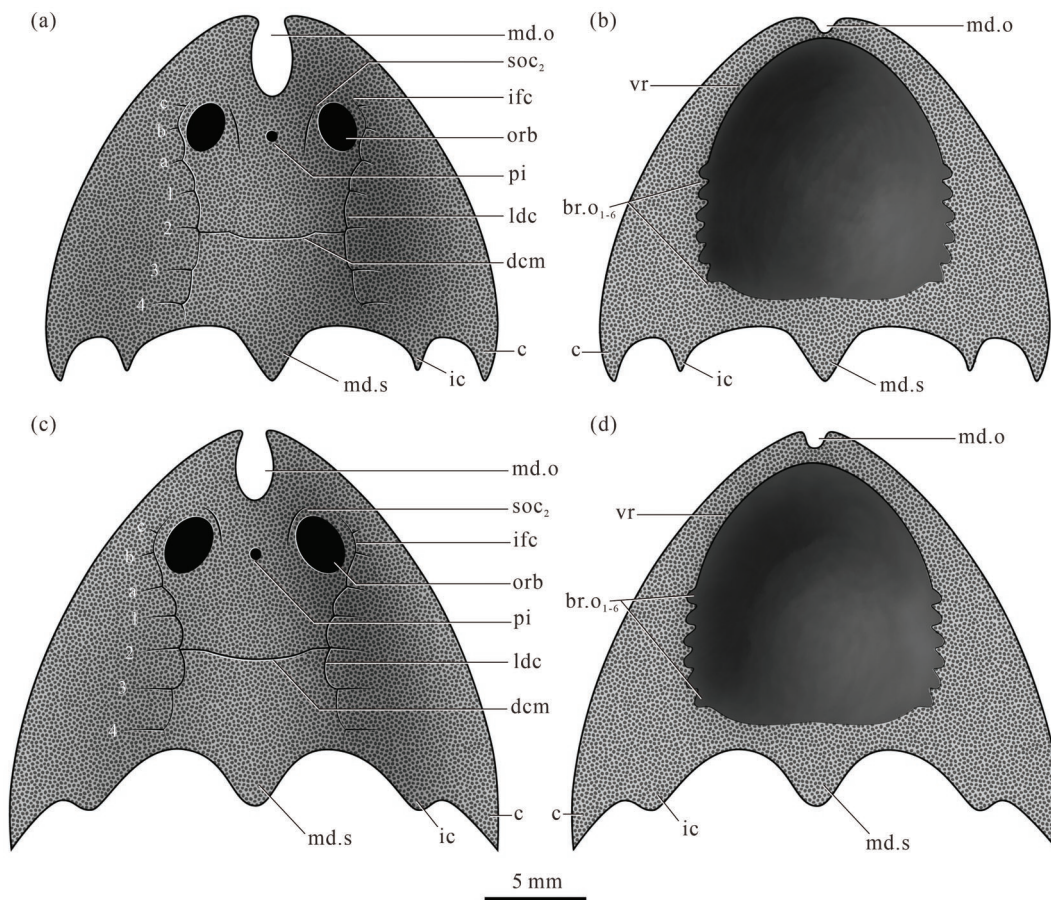


Fig. 5. Restoration of *Jiangxialepis jiujiangensis* sp. nov. and *Jiangxialepis retrospina*. Art credit: Shi Aijuan.
(a, b) The headshield of *Jiangxialepis jiujiangensis* sp. nov., in dorsal view (a) and ventral view (b); (c, d) the headshield of *Jiangxialepis retrospina* (Liu et al., 2021a), in dorsal view (c) and ventral view (d). Abbreviations see Figs. 2, 3, 4 plus br.o—branchial opening.

formations in Yangtze region (Fig. 7) (Zhang, 1982; Chen and Rong, 1996; Zong et al., 2011, 2017). Although the fish horizon is a little lower than that of the Xiushan Fauna, the fish assemblages in Wuhan were still considered to be middle Telychian age because they all come from the Fentou Formation (Zhu and Wang, 2000; Zhao and Zhu, 2010, 2014; Zong et al., 2011, 2017; Liu et al., 2021a).

As early as 1989, Chen and Wu (1989) firstly realized that the LRBs are probably present in Wuhan area and called them the Houjiatang Formation. Liu et al. (2021b) and Zong et al. (2021, 2022) further identified a new set of Silurian red clastic rocks conformably underlying the Fentou Formation in eastern Wuhan, and called them ‘Qingshui Formation’ that is equivalent to the LRBs in South China. Their later findings of fish fossils i.e., *H. guodingshanensis*, *Hongshanaspis inexpectatus*, *S. wuchangensis*, *S. triangulatus*, *Sinacanthus* sp., *N. planispinatus*, and *Tarimacanthus bachuensis* in Gumushan and Lishan sections in Wuhan were all referred to the LRBs (Liu et al., 2021b; Zong et al., 2022). Actually, the fish assemblages from the Silurian of Wuhan are consistent with the Wentang Assemblage in the Yangtze region and the Tataertag Assemblage in the Tarim region. For example, *Jiangxialepis* belongs to Shuyuidae which is the sister to all

other Eugaleaspiformes (Shan et al., 2020, 2022a; Liu et al., 2021a). As a key member of the Wentang Assemblage, Shuyuidae are known exclusively from the Silurian LRBs of early Telychian age in Yangtze region (Fig. 6), i.e., *Shuyu* and *Meishanaspis* from the lower part of the Tangchiawu Formation in Northwest Zhejiang (Gai et al., 2005, 2011; Shan et al., 2022a), *Qingshuiaaspis* and *Jiangxialepis* from the Qingshui Formation in Northwest Jiangxi (Shan et al., 2022a). *Hanyangaspis* and *Hongshanaspis* are comparable to *Latirostraspis* from the Houjiatang Formation in East Anhui (Wang et al., 1980), *Konoceraspis* from the Rongxi Formation in Northwest Hunan (Pan, 1992), and *Kalpinolepis* and *Nanjiangaspis* from the Tataertag Formation in Tarim region (Wang et al., 1996, 2002), all of which belong to the Hanyangaspidae. *Sinacanthus* and *Neosinacanthus* are established mainly based on the remains of fin spines of chondrichthyans, and are known exclusively from the LRBs in Yangtze and Tarim regions. The vertebrate assemblage from the Silurian of Wuhan is characterized by the occurrence of Hanyangaspidae (basal galeaspid), Shuyuidae (basal Eugaleaspiformes), and Sinacanthidae, which are type members of the Wentang Assemblage. Thus, the fish-bearing layers in Wuhan can be correlated with the Rongxi Formation in Hunan, Qingshui Formation in Jiangxi, Houjiatang Formation in Anhui and

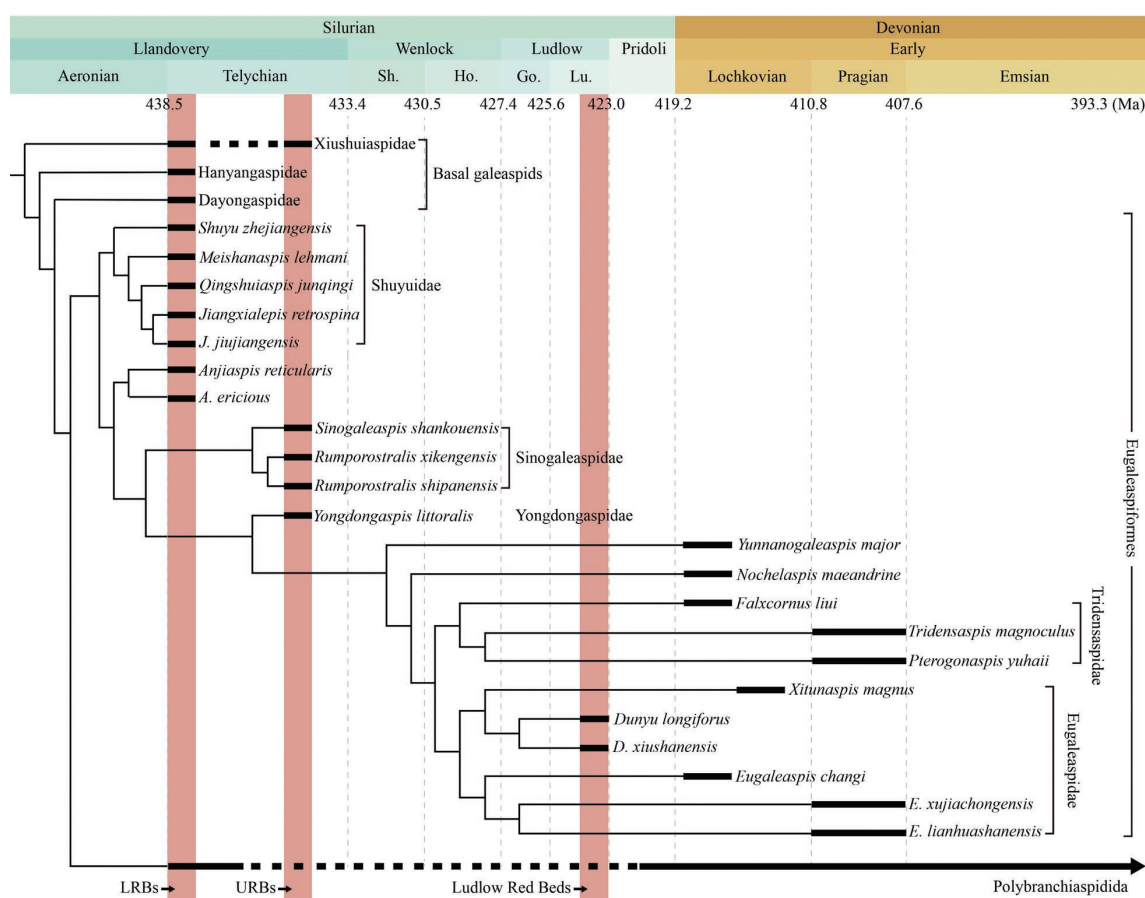


Fig. 6. A phylogenetic tree of Eugaleaspiformes projected against stratigraphy (based on Chen et al., 2022; Shan et al., 2022a; Sun et al., 2022; horizontal solid columns represent known time ranges, thin lines represent 'ghost range'; three vertical solid columns in red represent the geological range of Silurian marine red beds).

Abbreviations: Sh.–Sheinwoodian; Ho.–Homerian; Go.–Gorstian; Lu.–Ludfordian; LRBs–Lower Red Beds; URBs–Upper Red Beds.

System	Series	Stage	MRBs	Yangtze region										Tarim region					
				Northwest Zhejiang; Southeast Anhui	Northwest Jiangxi	Southeast Hubei	East Anhui; South Jiangsu	West Hubei	Northwest Hunan	North Guizhou	North Sichuan	Northeast Yunnan	Kalpin Xinjiang						
Silurian	Llandovery	Wenlock	Sheinwoodian	<div>★ Xiushan Fauna</div> <div>🐟 Wentang Assemblage</div>															
		Telychian	URBs																
	Aeronian	LRBs	?	★ Xiajiaqiao Fm.	★ Fentou Fm.	★ Fentou Fm.	Shamao Fm.	★ Xiushan Fm.		★ Yangpo-wan Mb.									
			🐟 Tangchiawu Fm.	🐟 Qingshui Fm.	🐟 Fentou Fm.	🐟 Houjiatang Fm.		🐟 Rongxi Fm.		🐟 Hanchiatien Fm.									
			Kangshan Fm.	Dianbei Fm.															
			Dabaidi Fm.	Lishuwo Fm.															

Fig. 7. Stratigraphical positions and correlations of the Silurian marine red beds in Yangtze and Tarim regions (modified after Rong et al., 2012, 2019; Shan et al., 2022b).

Abbreviations see Fig. 6 plus Fm.–Formation; Mb.–Member; MRBs–marine red beds.

Jiangsu, the Tangchiawu Formation in Zhejiang, and the Tataertag Formation in Tarim region. Therefore, their age should be modified as early Telychian (Fig. 7).

6 Conclusions

The occurrence of a new species, *Jiangxialepis jiujiangensis* sp. nov., in the early Telychian Qingshui Formation in Jiujiang, Jiangxi Province bears important morphological and biostratigraphic significance. The vertebrate fossils from the Silurian strata in Wuhan are type members of the Wentang Assemblage, which can be compared with fish fossils from the Rongxi Formation in Hunan, Qingshui Formation in Jiangxi, Houjiatang Formation in Anhui and Jiangsu, Tangchiawu Formation in Zhejiang, and Tataertag Formation in Tarim region. Therefore, their age should be modified as early Telychian, Llandovery, Silurian.

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