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A New Family of Galeaspids (Jawless Stem-Gnathostomata) from the Early Silurian of Chongqing, Southwestern China

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Abstract: A new genus and species of agnathan Eugaleaspidiformes (Galeaspida), *Yongdongaspis littoralis* gen. et sp. nov., is described from the Llandovery (lower Silurian) Huixingshao Formation at Yongdong Town, Xiushan County, Chongqing, southwestern China. This new Telychian taxon morphologically exhibits some transitional states between Sinogaleaspidae and a cluster of higher eugaleaspidiforms containing Tridensaspidae, Eugaleaspidae, *Yunnanogaleaspis,* and *Nochelaspis*, which we term here as the 'eugaleaspid cluster'. Phylogenetic analysis of an extended character matrix of Galeaspida reveals *Yongdongaspis*, on which Yongdongaspidae fam. nov. is erected, as the sister taxon of this 'eugaleaspid cluster', supported by two synapomorphies, the presence of one median transverse canal, and two lateral transverse canals leaving from the infraorbital canal. As the first fish described from the Llandovery Huixingshao Formation in Chongqing, *Yongdongaspis* provides new fossil evidence for the subdivision and correlation of the Upper Red Beds in South China.

Key words: vertebrate paleontology, Galeaspida, morphology, phylogeny, Telychian, Chongqing Municipality

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1 Introduction

The Silurian is an important period in the evolution of early vertebrates, characterized by the diversification and endemism of jawless (agnathan) fishes and the advent of jawed (gnathostomes) vertebrates (Zhu and Zhao, 2009; Brazeau and Friedman, 2015; Janvier, 2015; Zhao et al., 2018, 2021). As the first Paleozoic vertebrate found in Chongqing municipality, at the confluence of the Jialing and Yangtze rivers in southwestern China, *Eugaleaspis xiushanensis* was first found from the Silurian of Xiushan (formerly a county of Sichuan Province) by local geologists in 1962 (Liu, 1983; Zhu et al., 2012). Since then, no more Silurian fish material has been described from southeastern Chongqing except for a recent discovery from the Ludlow Xiaoxi Formation (Fm.) (Li et al., 2021), which also confirmed the Ludlow age of *E. xiushanensis*, although a large collection of early vertebrate fossils was known from coeval strata in neighboring areas, including Hunan (Pan and Zeng, 1985; Zeng, 1988; Wang, 1991a; Liu, 1997; Zhao et al., 2016), Guizhou (Sansom et al., 2000) and northwestern Jiangxi (Pan and Wang, 1980; Pan, 1986a, b; Gai and Zhu, 2005; Gai et al., 2005). Notably, a reappraisal of the holotype (IVPP V 6783.1) reassigned *Eugaleaspis xiushanensis* (Liu, 1983) to *Dunyu* (Zhu et al., 2012).

Since 2019, we have conducted a series of extensive field investigations and excavations in the Silurian strata of Xiushan, southeastern Chongqing, which eventually led to the discovery of many well-preserved fossil fishes, including galeaspids (jawless stem-Gnathostomata) from the Llandovery Rongxi and Huixingshao formations and the Ludlow Xiaoxi Fm., and jawed fishes from the Xiaoxi Fm. (Li et al., 2021). Remarkably, *Dunyu xiushanensis* was first described from a rolled stone at Shuiyuantou, about 15 km south of Yongdong, the source beds of which were assumed to be the Huixingshao Fm. Liu, 1983). Recent paleontological and stratigraphic work corroborated that the Ludlow Xiaoxi Fm. was the source of *D. xiushanensis* rather than the newly defined Huixingshao Fm. (Zhu et al., 2012; Li et al., 2021).

Here we describe the first galeaspid material from one site in the Huixingshao Fm. at Yongdong Town, Xiushan County, Chongqing Municipality, southwestern China (Fig. 1).

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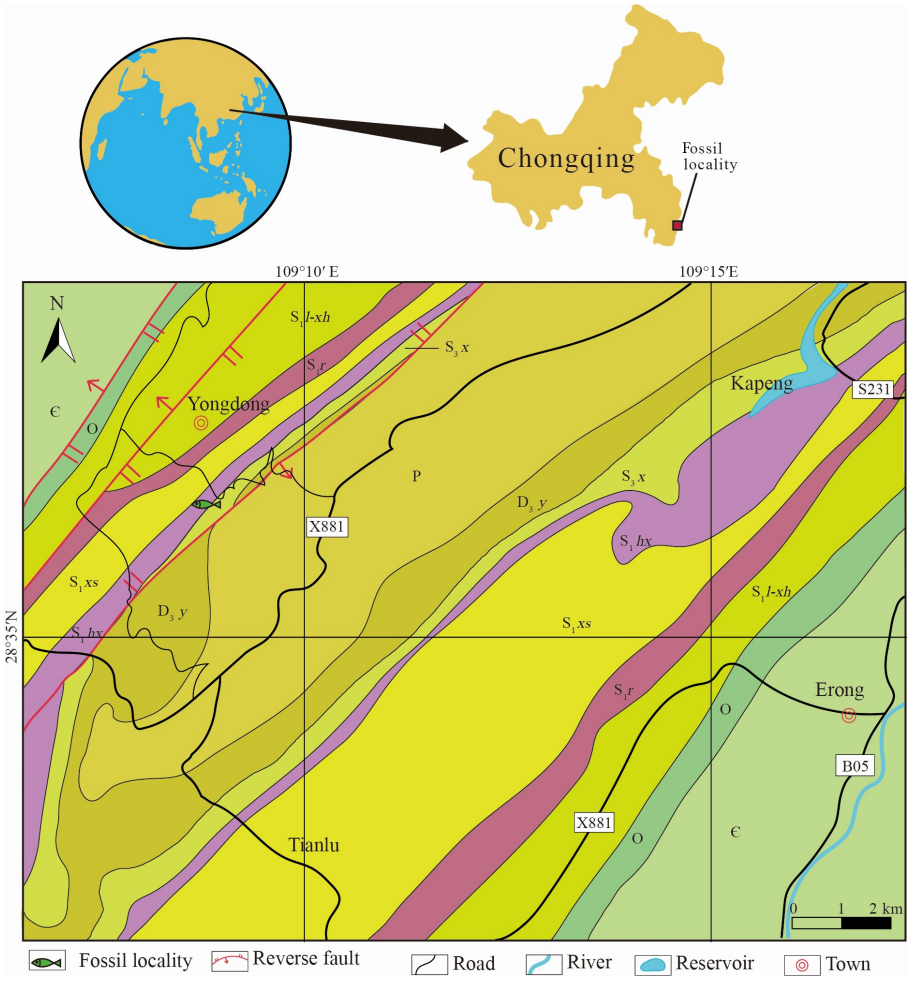

Fig. 1. Regional geological map of the *Yongdongaspis* fossil site in Chongqing Municipality, southwestern China.
Abbreviations: Є, Cambrian; O, Ordovician; Silurian, S_1l-*xh*, Longmaxi Fm. + Xintan Fm.+ Xiaoheba Fm.; S_1r, Rongxi Fm.; S_1xs, Xiushan Fm.; S_1hx, Huixingshao Fm.; S_3x, Xiaoxi Fm.; Devonian, D_3y, Yuntaiguan Fm.; P, Permian.

2 Geological Setting

The stratigraphic column of the fossil site at Yongdong consists of the lower Silurian, Llandovery Rongxi, Xiushan, Huixingshao formations and the upper Silurian, Ludlow Xiaoxi Fm. (Fig. 2). The Xiaoxi Fm. contacts disconformably with both the underlying and overlying beds (Wang et al., 2010; Wang, 2011). The Huixingshao Fm. is mainly comprised of thin-bedded red and yellow-green siltstone and mudstone and is conformably underlain by the Xiushan Fm. and disconformably overlain by the Xiaoxi Fm. The galeaspids from the Huixingshao Fm. in this new fossil site include the new taxon described here, and several other new forms under study.

The fish-bearing Huixingshao Fm. forms part of the Upper Red Beds (URBs) in South China and is the equivalent of the Xikeng Fm. in Jiangxi, and the Maoshan Fm. in the Jiangsu and Zhejiang provinces (Rong et al., 2019). An invertebrate shelly fauna from the underlying Xiushan Fm. and sequence stratigraphic analyses indicate that the age of the Huixingshao Fm. is middle–late Telychian (Zhao et al., 2009; Zhao and Zhu, 2010; Wang et al., 2018; Rong et al., 2019).

3 Material and Methods

The new material includes 47 headshields of *Y. littoralis* (CIGMR V0101-V0124 and IVPP V28714-V28736, Figs. 3–4). All these specimens are permanently housed and accessible for examination in the collections of the Chongqing Institute of Geology and Mineral Resources (CIGMR) and the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Beijing.

All specimens were prepared mechanically using a Vibro-tool with a tungsten-carbide bit or a needle. Specimens were measured with a digital vernier caliper, studied under an Olympus SZ16 zoom stereomicroscope, and photographed with a Nikon D810 camera with a Nikon micro photo lens (AF-S MICRO NIKKOR 105 mm 1: 2.8G ED). Phylogenetic data were entered and coded in Mesquite 3.61 (Maddison and Maddison, 2019), and then exported as a TNT file. Parsimony analysis was performed in TNT v 1.5 (Goloboff and Catalano, 2016) using traditional search and TBR branch swapping. Branch support was estimated with the bootstrap values by 100 pseudoreplicates and Bremer decay indices. All characters were unordered and weighted equally, as in the earlier

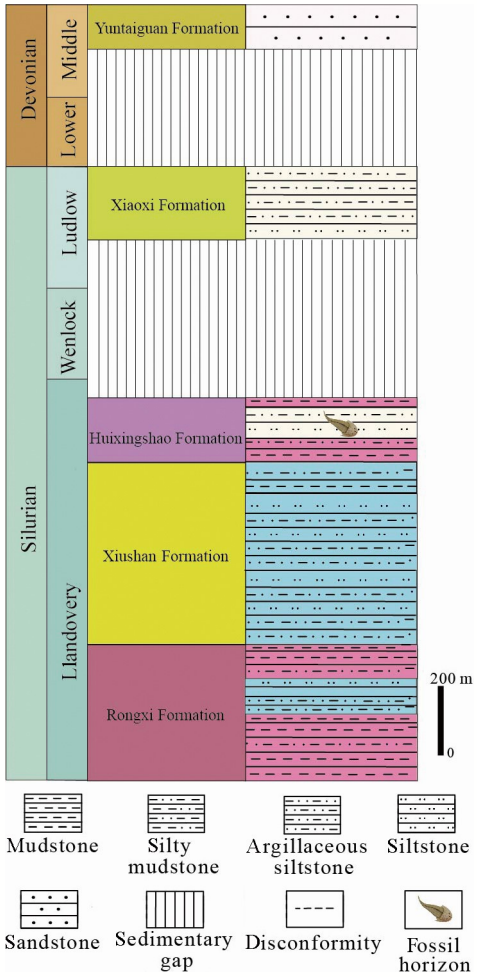

Fig. 2. Stratigraphic column showing the horizon yielding the type specimen of *Yongdongaspis littoralis* gen. et sp. nov.

versions of this dataset. An early plesiomorphic non-cornuate osteostracan (also a jawless stem-gnathostome) *Ateleaspis* (Sansom, 2009) was selected as the outgroup for our phylogenetic analysis. The analysis yielded five equivalent most-parsimonious trees (Fig. 5) with a tree length of 194, consistency index (CI) of 0.418, and retention index (RI) of 0.767.

4 Results

4.1 Systematic paleontology

Subclass Galeaspida Tarlo, 1967

Order Eugaleaspidiformes (Liu, 1965) Liu, 1980

Family Yongdongaspidae Chen, Gai, Li and Zhu fam. nov.

Diagnosis: As for *Yongdongaspis* Chen, Gai, Li and Zhu gen. nov.

Remarks: Phylogenetic analysis recovers *Yongdongaspis* as the sister taxon to the clade containing Tridensaspidae, Eugaleaspidae, *Yunnanogaleaspis,* and *Nochelaspis*. This placement is supported by two synapomorphies, the presence of one median transverse canal, and two lateral transverse canals leaving from infraorbital canal. In this paper, we term the clade containing Tridensaspidae, Eugaleaspidae, *Yunnanogaleaspis* and *Nochelaspis* the 'eugaleaspid cluster', and erect a new family, Yongdongaspidae fam. nov. for *Yongdongaspis*.

Genus *Yongdongaspis* Chen, Gai, Li and Zhu gen. nov.

Etymology: *Yongdong*, after the fossil site in Xiushan, Chongqing, China, and *aspis* (Gr.), shield.

Type species: *Yongdongaspis littoralis* Chen, Gai, Li and Zhu sp. nov.

Diagnosis: As for the only species.

Remarks: *Yongdongaspis* is characterized by a character combination intermediate between Sinogaleaspidae and the 'eugaleaspid cluster'.

Yongdongaspis littoralis Chen, Gai, Li and Zhu sp. nov.

Holotype: A nearly complete headshield, CIGMR V0101A, B (Fig. 3a–b).

Referred specimens: 17 complete or nearly complete headshields, CIGMR V0102–V0110, IVPP V28714–V28721; and 29 incomplete headshields CIGMR V0111–V0124, IVPP V28722–V28736 (Figs. 3c–f, 4a–d).

Etymology: From *littoralis* (Latin), near-shore, in reference to the near-shore niche of the fish. **Diagnosis:** Small-sized subtriangular headshield with its highest point at the posterior margin, length-to-width ratio of about 0.9; spine-shaped cornual processes caudo-laterally oriented, broad leaf-shaped inner cornual processes caudally oriented; longitudinal oval-like median dorsal opening extending anteriorly near the rostral margin of the headshield and posterior to the level of the center of orbital opening; pineal opening slightly behind the posterior margin of the orbital opening; a forked preorbital commissure consisting of anterior supraorbital canal, posterior supraorbital canal and a short vestige of the infraorbital canal; median dorsal canal joining smoothly with the posterior supraorbital canal behind the level of pineal opening, and posteriorly converging with the opposite one to form a U-shaped trajectory; one dorsal commissure developed; a short central canal issued from the U-shaped median dorsal canal; two lateral transverse canals issued from the infraorbital canal; pear-shaped cavity for the oral fenestra and branchial fenestra; six notches for the branchial openings.

Type locality and horizon: Yongdong, Xiushan County, Chongqing Municipality, southwestern China; Huixingshao Fm., Telychian, late Llandovery, Silurian.

4.2 Description

Yongdongaspis littoralis is a small eugaleaspid with a subtriangular headshield (Figs. 3–7). In dorsal view, the headshield is gently arched to form a bilaterally symmetrical domed structure with its highest point at the posterior margin. The rostral margin of the headshield is arciform and lacks a rostral process. The measurements of *Y. littoralis* indicate that the headshield is shorter than it is wide with a length-to-width ratio of about 0.9 (Table 1). The headshield protrudes caudally into a pair of cornual (c, Fig. 3a–f) and inner cornual processes (ic, Fig. 3a–b). The cornual process is short, extends caudo-laterally, and

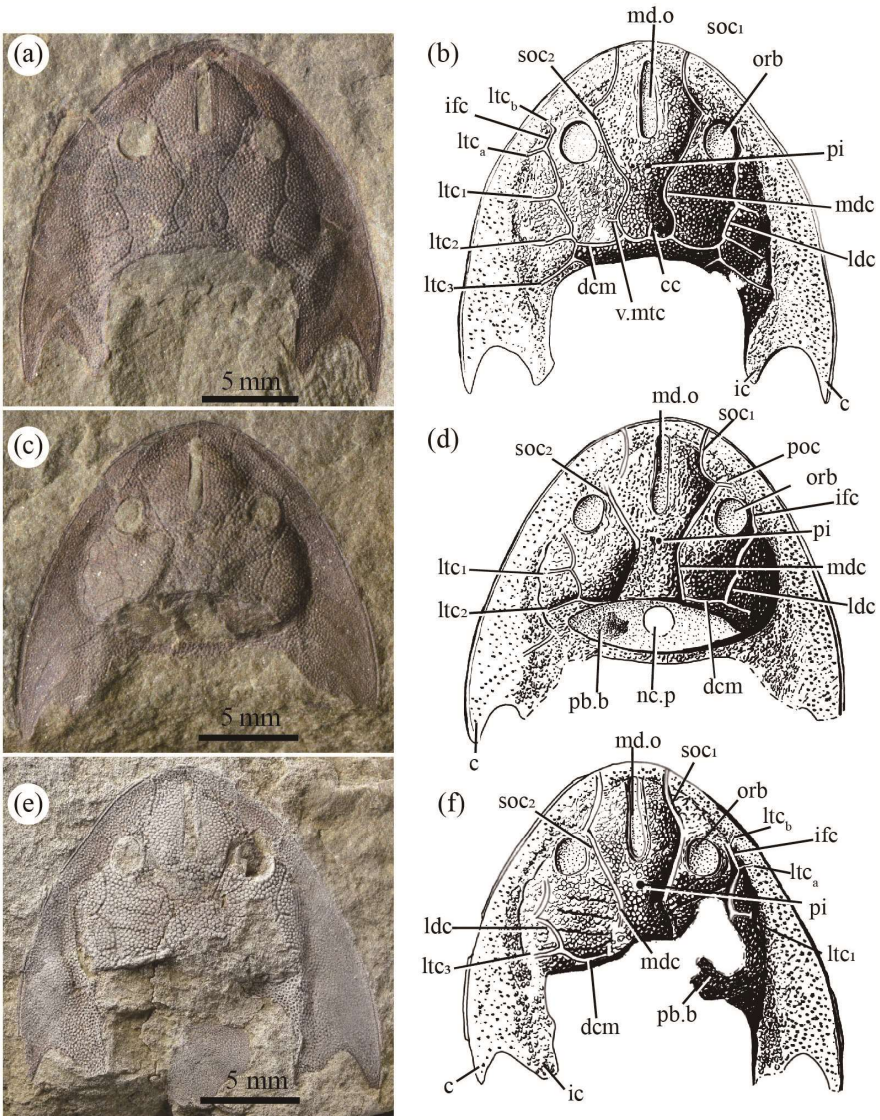

Fig. 3. Photographs (a, c, e) and interpretative drawings (b, d, f) of the headshield of *Yongdongaspis littoralis* gen. et sp. nov. in dorsal view: (a, b) a complete internal mold of the holotype, CIGMR V0101A; (c, d) a nearly complete internal mold of paratype, CIGMR V0102 A; (e, f) a nearly complete internal mold of paratype, CIGMR V0103 A.

Abbreviations: c, cornual process; cc, central canal; dcm, dorsal commissure; ic, inner corneal process; ifc, infraorbital canal; ldc, lateral dorsal canal; ltc, lateral transverse canal; mdc, median dorsal canal; md.o, median dorsal opening; nc.p, pore for the passage of the notochordal canal; orb, orbital opening; pb.b, postbranchial bar; pi, pineal opening; poc, preorbital commissure; soc_1, anterior supraorbital canal; soc_2, posterior supraorbital canal; v.mtc, vestige of the median transverse canal.

tapers off rapidly in the holotype and referred specimens. The inner cornual process is small, broad leaf-shaped, and caudally oriented. The inner cornual process is shorter and wider than the cornual process.

The median dorsal opening (md.o, Fig. 3a–f) is a longitudinal oval with its length-to-width ratio of about 5.0 (Table 1). The anterior end of the opening extends to near the rostral margin of the headshield and its posterior end is positioned near the level of the center of orbital opening.

The round orbital openings (orb, Fig. 3a–f) are dorsally positioned on the headshield and with a diameter of about 1.7 mm among the 24 specimens (Table 1). The orbital openings in some specimens are near-oval, due to postmortem deformation (Fig. 3a–d).

The small and round pineal opening (pi, Fig. 3a–f), with a diameter of 0.5 mm, is slightly behind the posterior margin of the orbital opening in the midline of the headshield. The ratio of the length of the pre-pineal and post-pineal region is about 1.36 (Table 1).

The sensory canal system is comprehensively reconstructed based on the 36 specimens that preserve the dorsal aspect (Figs. 6, 7). The sensory canals consist of anterior supraorbital, posterior supraorbital, infraorbital, lateral dorsal, lateral transverse, median dorsal, and median transverse canals, a preorbital commissure and a short central canal (Fig. 3a–f). The paired anterior supraorbital canals (soc_1) diverge posteriorly from the rostral margin and connect with the posterior supraorbital canals (soc_2) and a short vestige of the infraorbital canals

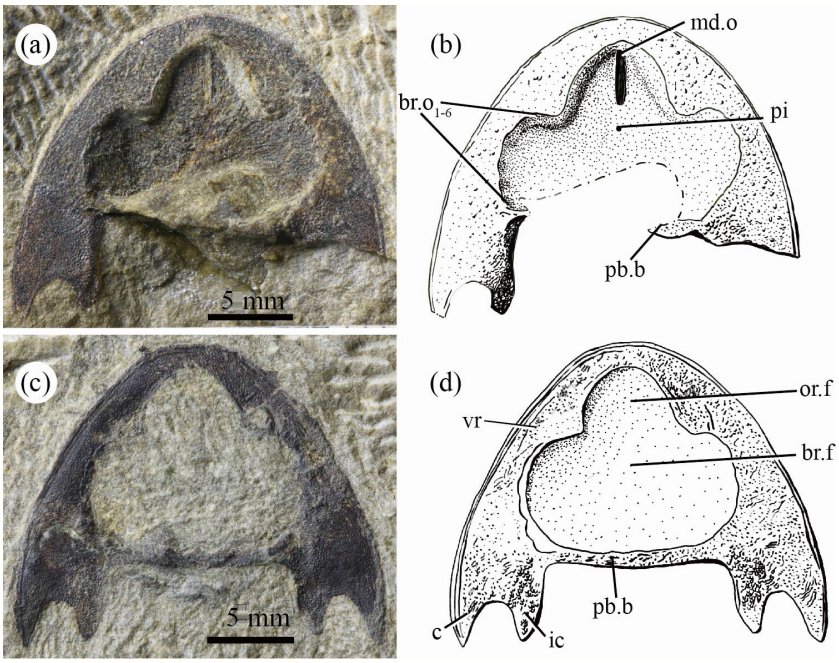

Fig. 4. Photographs (a, c) and interpretative drawings (b, d) of the headshield of *Yongdongaspis littoralis* gen. et sp. nov. in ventral view: (a, b) a complete nearly external mold of paratype, CIGMR V0112 A; (c, d) a nearly complete external mold of paratype, CIGMR V0120.
Abbreviations: c, cornual process; ic, inner corneal process; br.f, branchial fenestra; br.o, branchial opening; md.o, median dorsal opening; or.f, oral fenestra; pb.b, postbranchial bar; pi, pineal opening; vr, ventral rim.

(ifc) to form a forked preorbital commissure (poc, Fig. 3c–d). The median dorsal canal (mdc, Fig. 3a–f) joins smoothly with the posterior supraorbital canal (soc_2) in about 120 degrees behind the level of pineal opening, and posteriorly curves inward to converge with the opposite one to form a U-shaped trajectory. Only one dorsal commissure (dcm, Fig. 3a–f) is present to connect the median dorsal and lateral dorsal canals, and a vestige of the median transverse canal (v.mtc, Fig. 3a–b) branches from the median dorsal canals. A short central canal (cc, Fig. 3a–b) is issued from the U-shaped median dorsal canal. The infraorbital canal (ifc, Fig. 3a–f) is laterally positioned to the orbital opening. Posteriorly, the infraorbital canal continues to extend as the lateral dorsal canal (ldc, Fig. 3a–f), which is the main longitudinal canal on the headshield. There are five pairs of lateral transverse canals (ltc, Fig. 3a–b, e–f). The anterior two transverse canals (ltc_a, ltc_b, Fig. 3a–b, e–f) are positioned lateral to the orbital opening. The most posterior lateral transverse canal (ltc_3, Fig. 3a–b, e–f) is positioned near the posterior edge of the headshield.

In ventral view, the well-preserved ventral rim (vr, Fig. 4a–d) and an extensive postbranchial bar (pb.b, Figs. 3c–d, 4c–d) encloses a large pear-shaped cavity for the oral fenestra (or.f, Fig. 4c–d) and branchial fenestra (br.f, Fig. 4c–d). Starting from the oral margin, the ventral rim gets broader till the level of the boundary between the oral fenestra and branchial fenestra. The length of the oral fenestra is about 3.9 mm, whereas its maximum width is about 5.5 mm (Table 2). The maximum length of the branchial fenestra is about 6 mm and the maximum width is about 11.7 mm (Table 2). The ventral rim is narrowest at the level of the second and third branchial fossae, and gradually becomes wider to the level of the last branchial fossa (Fig. 4a–b). The part of the ventral rim contributing to the branchial openings is comparatively wide, in contrast to the condition in *Dunyu longiforus* (Zhu et al., 2012), yet similar to that in *Eugaleaspis xujiachongensis* (Liu, 1975). Along the margin of the branchial fenestra, six notches for the branchial openings ($br.o_{1–6}$, Fig. 4a–b) are discernable, as in other eugaleaspidiforms.

The endoskeletal roof of the oral fenestra and branchial fenestra is poorly preserved in the internal mold. However, in some specimens, the head is posteriorly penetrated by a large pore for the passage of the notochordal canal (nc.p, Fig. 3c–d), with a diameter of about 1.6 mm (Table 1).

The lateral margin of the headshield is smooth and the surface of the headshield is uniformly ornamented with closely set, fine, rounded granular tubercles with a diameter of about 0.2 mm (Fig. 3c). There are about 22 tubercles per square millimeter.

4.3 Phylogenetic results

A previous analysis (Shan et al., 2020) indicated that the Eugaleaspidiformes is a monophyletic group composed of the Shuyuidae (Shan et al., 2020), Sinogaleaspidae (Pan and Wang, 1980), Tridensaspidae (Liu, 1986), Eugaleaspidae (Liu, 1980), and an Incertae Familiae comprising *Yunnanogaleaspis* and *Nochelaspis*.

In order to explore the position of *Yongdongaspis*, a new phylogenetic analysis was conducted based on previous datasets (Gai and Zhu, 2005; Zhu and Gai, 2006; Gai et al., 2018; Gai et al., 2020; Shan et al., 2020; Jiang et al., 2021). One new character was added:

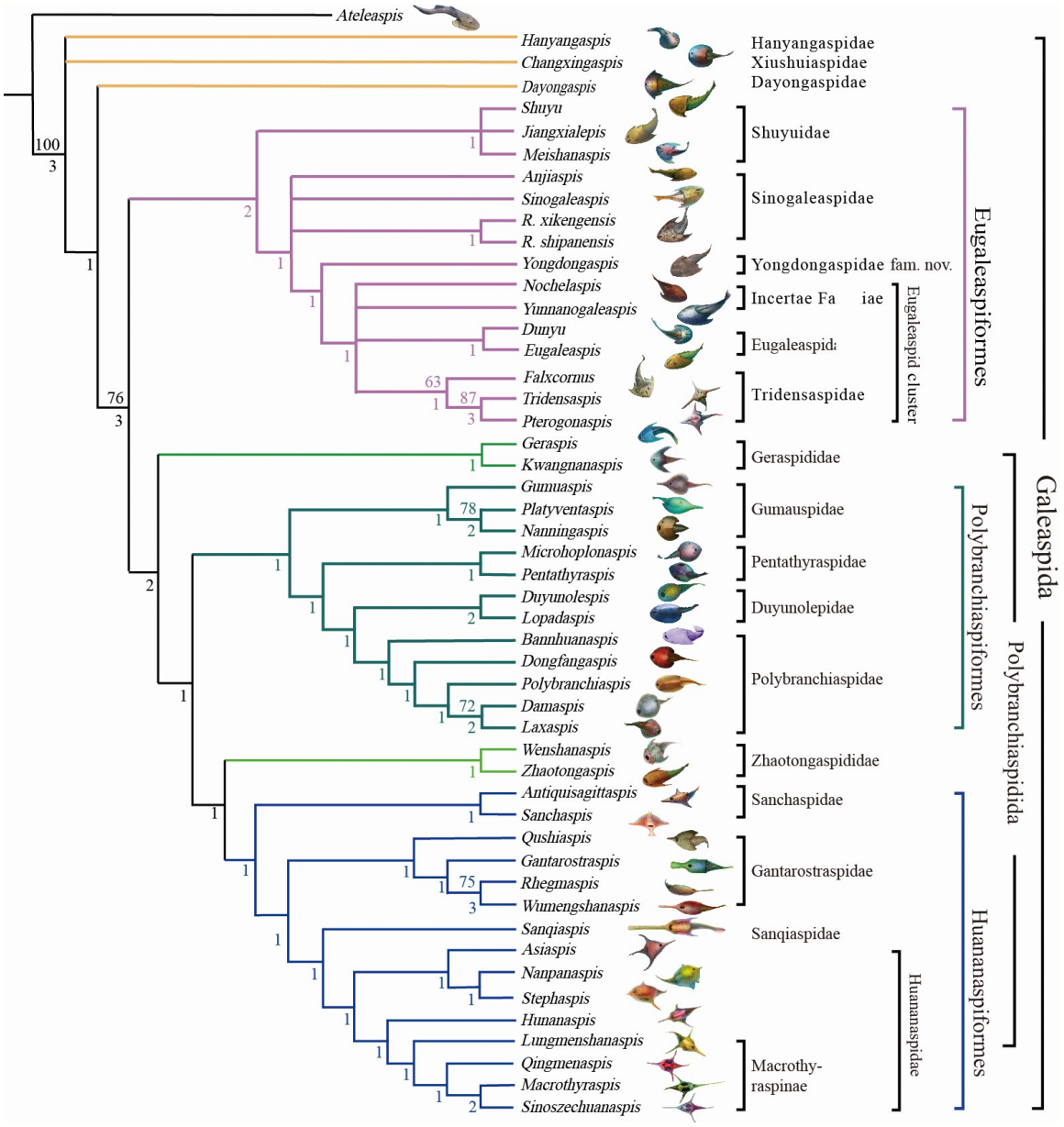

Fig. 5. Strict consensus tree of five most parsimonious trees with a cladistically based classification of the Galeaspida. Tree length = 194, consistency index (CI) = 0.418, retention index (RI) = 0.767, Numbers on branches denote bootstrap frequencies (above node) and Bremer support values (below node), bootstrap frequencies below 50 are not shown (analysis based on the dataset revised from Gai and Zhu, 2005; Zhu and Gai, 2006; Gai et al., 2018; Gai et al., 2020; Shan et al., 2020; Jiang et al., 2021). Artwork credit, Dinghua Yang.

[64] central canal (cc): (0) absent; (1) present.

The new phylogenetic analysis supports the previous results and corroborates that besides Shuyuidae, Sinogaleaspidae, and Yongdongaspidae, the remaining members of the Eugaleaspidiformes form a 'eugaleaspid cluster', while *Yongdongaspis* is positioned as the sister taxon to this cluster (Fig. 5). *Yongdongaspis* and the 'eugaleaspid cluster' together differ from the other basal Eugaleaspidiformes, i.e., Shuyuidae and Sinogaleaspidae, in the U-shaped posterior supraorbital canals and only one median transverse canal. It is noteworthy that the Tridensaspidae, Eugaleaspidae, and the Incertae Familiae that contains *Yunnanogaleaspis* and *Nochelaspis* form a trichotomy in the resulting strict consensus tree.

5 Discussion

5.1 Morphological implication

Yongdongaspis can be referred to the Eugaleaspidiformes because it exhibits a suite of diagnostic characters for this order, including the triangular headshield, longitudinal oval-like median dorsal opening, and typical eugaleaspid-pattern sensory canal system (Zhu, 1992; Gai and Zhu, 2005; Zhu and Gai, 2006; Gai et al., 2018), while exhibiting a mélange of primitive and derived characters in the overall shape and the pattern of sensory canals.

Yongdongaspis bears a close resemblance to *Yunnanogaleaspis* (Pan and Wang, 1980) and *Nochelaspis*

Table 1 Measurements of *Yongdongaspis littoralis* gen. et sp. nov in dorsal aspect (in mm)

Item	Max. length of headshield	Max. width of headshield	Length of headshield in midline	Diameter of orbital opening	Distance between orbital openings	Long axis of median dorsal opening	Short axis of median dorsal opening	Length of pre-pineal region in midline	Length of post-pineal region in midline
CIGMR V0101	17.1	18.8	10	2	5.4	3.5	0.8	5.5	4.5
CIGMR V0102	16.4	18.7	8.7	1.5	5.5	3.8	0.71	5.9	2.8
CIGMR V0103	17.6	19.4	9.7	1.5	5.9	3.6	0.82	5.5	4.2
CIGMR V0104	—	17.8	—	1.62	5.8	—	0.97	—	5.1
CIGMR V0105	16	19.1	9.9	1.52	5.3	3	0.55	5.7	4.2
CIGMR V0106	16.6	—	8.9	1.45	6	3.8	0.79	5.7	4.2
CIGMR V0007	—	—	9.2	1.77	5.6	3.5	0.74	5.7	3.5
CIGMR V0008	20.2	21.6	13.4	1.30	5.6	4.4	0.91	6.1	7.3
CIGMR V0013	—	19.5	10.7	1.81	5.2	4.4	0.63	6.5	4.2
CIGMR V0114	15.9	—	9.9	1.59	5.5	3.3	0.79	5.6	4.3
CIGMR V0115	16.2	—	—	—	—	—	0.68	—	—
CIGMR V0116	16.3	19.2	8.6	1.92	—	—	—	5.1	3.5
CIGMR V0117	18	—	10.5	1.71	5.2	3.8	0.89	5.7	4.8
CIGMR V0118	18.2	—	11.2	1.67	5.7	4.2	0.81	6.4	4.8
CIGMR V0119	—	19.4	—	—	—	—	—	—	—
CIGMR V0120	18.6	20.3	10.4	1.75	5.6	4	0.82	6	4.4
CIGMR V0121	16.2	—	9.8	1.73	5.5	3.9	0.92	5.6	4.2
CIGMR V0122	16.4	17.6	—	1.53	—	3.2	0.73	—	—
CIGMR V0123	17.3	19.1	9.7	1.25	5.7	3.5	0.63	5.8	3.9
CIGMR V0124	—		9.2	1.71	5.4	3.7	0.63	6.1	—
IVPP V28714	16.7	18.4	9.4	1.71	5.6	3.3	0.75	5.2	4.2
IVPP V28715	—	—	9.7	1.75	5.4	3.7	0.62	6.2	3.5
IVPP V28716	—	—	10.96	1.86	5.1	4.1	0.81	6.6	4.36
IVPP V28717	16.4	17.1	9.3	1.59	5.7	—	—	5.8	3.5
IVPP V28718	16.4	17.9	10.1	1.52	5.2	4.1	0.73	—	—
IVPP V28719	17.4	19.3	10.3	1.62	5.4	3.8	0.75	5.7	4.6
IVPP V28720	16.1	—	9.5	1.34	4.8	3.7	0.63	5.2	4.3
IVPP V28721	—	—	—	1.86	5.5	3.9	0.8	5.5	—
IVPP V28722	17.7	—	—	1.94	4.5	4	0.59	6.1	—
IVPP V28723	14.2	—	9.1	1.38	4.9	3.1	0.73	5	4.1
IVPP V28724	—	—	—	1.87	—	3.1	0.62	5.1	—
IVPP V28725	17	—	9.9	1.91	5.5	4	0.77	6.2	3.7
IVPP V28726	18.5	—	—	1.86	5.6	4	0.79	6.5	—
IVPP V28727	18.7	—	—	1.92	5.6	4	0.78	6.5	—
IVPP V 28728	15.8	19.6	—	1.49	5.2	3.7	0.53	5.7	—
IVPP V28729	—	18.3	—	2.02	5.1	4.1	0.7	6	—

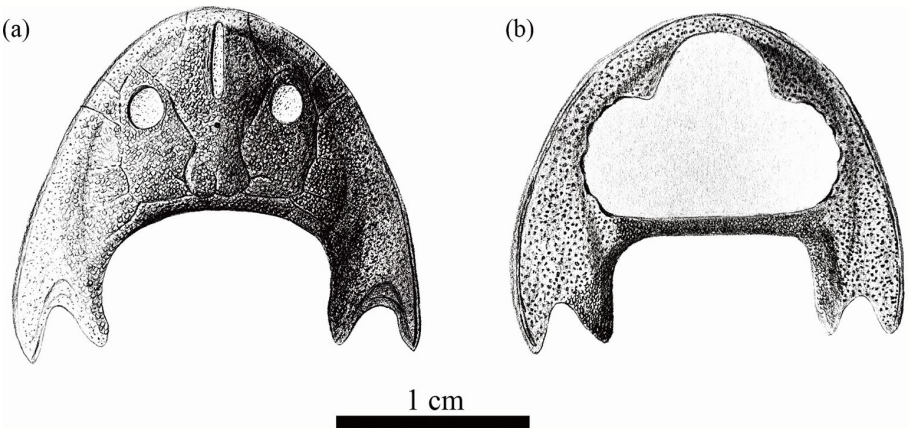

Fig. 6. Restoration of *Yongdongaspis littoralis* gen. et sp. nov. in (a) dorsal view; and (b) ventral view.

(Zhu, 1992) with its subtriangular headshield, a longitudinal oval-like median dorsal opening, U-shaped medial dorsal canal, three lateral transverse canals running from the lateral dorsal canal, spine-shaped cornual and broad leaf-shaped inner cornual processes. The primary difference is that in *Yongdongaspis* the median dorsal opening extends posteriorly near the level of the center of the orbital opening and anteriorly near the rostral margin of the headshield. The extended median dorsal opening can be observed in *Sinogaleaspis shankouensis* (Gai et al., 2020) and most of the 'eugaleaspid cluster', *Dunyu* in particular, which extends posteriorly beyond the posterior margin of the orbital opening (Zhu et al., 2012). Zhu and Gai (2006) considered that the extension of the median dorsal opening corresponds to the transformation of the median dorsal opening from longitudinal oval to longitudinal slit in the Eugaleaspidiformes. Therefore, the longitudinal oval median dorsal opening in *Yongdongaspis*

Table 2 Measurements of *Yongdongaspis littoralis* gen. et sp. nov in ventral aspect (in mm)

Item	Max. length of headshield	Max. width of headshield	Length of headshield in midline	Max. length of oral fenestra	Max. width of oral fenestra	Max. length of branchial fenestra	Max. width of branchial fenestra
CIGMR V0109	16.4	—	12	3.8	6.2	6.4	12.6
CIGMR V0110	16.7	20.5	12.2	3.9	5.5	6.4	11.8
CIGMR V0111	15.6	—	11.7	3.9	5.6	5.9	—
CIGMR V0112	—	—	12.6	4.3	—	5.9	—
IVPP V28730	16.7	18.2	12	4.3	5.5	5.2	11.7
IVPP V28731	17	18.4	11.8	3.8	5.5	5.8	11.8
IVPP V28732	16.9	18.1	12	3.8	4.5	6.2	11.2
IVPP V28733	16.5	18.1	11.6	3.7	5.4	6.2	10.9
IVPP V28734	16.6	17.7	11.6	3.8	5.8	6.1	11.6
IVPP V28735	18.4	—	12	3.5	5.8	6.2	—
IVPP V28736	—	19.2	—	4	5.1	5.3	11.8

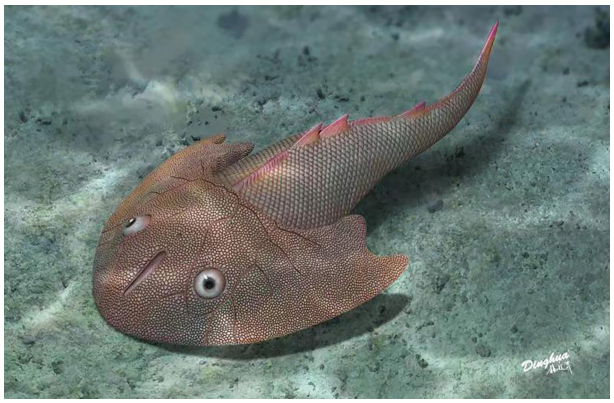

Fig. 7. Possible life reconstruction of *Yongdongaspis littoralis* gen. et sp. nov.
The reconstruction of the post-cephalopectoral body is based on *Sinogaleaspis shankouensis* (Shan et al., 2020). Art credit, Yang Dinghua.

can be considered plesiomorphic.

Yongdongaspis has two pairs of lateral transverse canals branching from the infraorbital canals, a condition strikingly similar to that of the Sinogaleaspidae, Shuyuidae and some plesiomorphic taxa such as *Changxingaspis*, *Dayongaspis* and *Hanyangaspis* (Liu, 1979; Pan and Wang, 1980; Pan and Zeng, 1985; Gai et al., 2011, 2020; Shan et al., 2020). In the 'eugaleaspid cluster' except *Yunnanogaleaspis*, the lateral transverse canals emerging from the infraorbital canals are absent. Gai et al. (2005) suggested that reduction of lateral transverse canals represents a character polarity in the Eugaleaspidiformes, which means that the eugaleaspidiform lateral transverse canals tend to decrease gradually.

Yongdongaspis differs markedly from Eugaleaspidae in the presence of an inner cornual process. Zhu (1992) indicated that the inner cornual process is common in the outgroup of eugaleaspidiforms, and, therefore, the presence of an inner cornual process is considered to be a plesiomorphic condition, whereas the absence of the inner cornual process in Eugaleaspidae is apomorphic. This supports the plesiomorphic status of *Yongdongaspis* relative to the 'eugaleaspid cluster'.

There is a short median transverse canal branching from the middle dorsal canal in *Yongdongaspis*. Over one median transverse canal is regarded as a primitive feature found in plesiomorphic galeaspid taxa such as Dayongaspidae, Hanyangaspidae, Xiushuiaspidae and Sinogaleaspidae (Pan and Wang, 1980, 1983; Wang, 1991b; Gai et al., 2005, 2020; Shan et al., 2020), whereas in the 'eugaleaspid cluster', only one median transverse canal remained. This remanent feature further implies that *Yongdongaspis* is a plesiomorphic taxon relative to the 'eugaleaspid cluster' (Fig. 5).

5.2 Biostratigraphic significance

Telychian marine red beds are well developed in South China (Rong et al., 2012; Zhang et al., 2018), and consist of the early Telychian Lower Red Beds (LRBs), middle-late Telychian Upper Red Beds (URBs), and Ludlow Red Beds. In South China and Tarim, Silurian red beds are composed of intercalated purple-red and yellowish-green layers, deposited in shallow marine settings and these are used as an important marker in regional stratigraphic subdivisions and correlation (Ge et al., 1979; Rong et al., 2019).

In northeastern Guizhou, southeastern Chongqing, and northwestern Hunan (Ge et al., 1979), the LRBs are called the Rongxi Fm., and the URBs are called the Huixingshao Fm. Stratigraphically, the Rongxi, Xiushan and Huixingshao formations constitute a continuous sequence in ascending order (Rong et al., 1990). The upper part of the Xiushan Fm. yields a well-known Xiushan Fauna of middle Telychian age (Rong et al., 2003, 2007, 2019) and, therefore, the age of the Rongxi Fm. (LRBs) is regarded as the early Telychian to latest Aeronian and the Huixingshao Fm. (URBs) is thought to be the middle-late Telychian in age.

Because of the lack of decisive fossil evidence, the definition, the subdivision and the correlation of the Huixingshao Fm. have been debated for decades (Wang et al., 2010). It was first defined as a set of purplish-red and grayish-yellow argillaceous siltstones, which were conformably underlain by the middle Telychian Xiushan Fm. and unconformably overlain by the Givetian (Middle Devonian) Yuntaiguan Fm. (Rong et al., 1990). Recent stratigraphic studies (Wang et al., 2010; Wang, 2011) revealed that the original Huixingshao Fm. in Chongqing and Guizhou can be subdivided into two parts: the upper bearing grayish-yellow mudstones and siltstones as the Ludlow–Pridoli Xiaoxi Fm., and the lower bearing purplish-red siltstones and mudstones as the middle-late Telychian Huixingshao Fm. This subdivision scheme was mainly based on microfossils and large stout tubular trace fossils (Wang et al., 2011). Meanwhile, the difference in lithology between the Xiaoxi Formation and the underlying Huixingshao Fm. is less obvious, causing

difficulty at the outcrops in locating the lithostratigraphic boundary between the two formations.

As noted, the middle-late Telychian Huixingshao Fm., which yields *Yongdongaspis*, is equivalent to the Xikeng Formation in Jiangxi Province, and the Maoshan Fm. in Jiangsu and Zhejiang provinces. To date, there are eight genera within the Eugaleaspidiformes found in this set of strata. Besides the newly found *Yongdongaspis* in the Huixingshao Fm., the Xikeng Fm. has yielded *Rumporostralis*, *Sinogaleaspis*, *Xiushuiaspis* (Pan and Wang, 1980, 1983; Pan, 1986a; Gai et al., 2020; Shan et al., 2020) , and in the Maoshan Fm., *Anjiaspis*, *Meishanaspis*, *Shuyu*, *Changxingaspis* (Pan and Wang, 1980; Wang, 1991b; Gai and Zhu, 2005; Gai et al., 2005; Gai et al., 2011; Gai, 2018; Gai et al., 2019), all of which have been assigned as either basal galeaspids or Sinogaleaspidae, whereas *Yongdongaspis* represents the sister taxon of the 'eugaleaspid cluster', which otherwise has the earliest occurrence in the Ludlow. Positioned between the Sinogaleaspidae and the 'eugaleaspid cluster', *Yongdongaspis* in the Huixingshao Fm. provides new fossil evidence for the subdivision and correlation of the URBs in South China. In between, there is a long apparent hiatus in the Wenlock where it would be good to locate new suitable outcrops in China.

6 Conclusions

The new taxon, *Yongdongaspis littoralis* gen. et sp. nov., has been found in the middle-late Telychian Huixingshao Formation in Chongqing Municipality, southwestern China. Morphologically, *Y. littoralis* exhibits certain transitional states between Sinogaleaspidae and a cluster of higher eugaleaspidiforms termed here the 'eugaleaspid cluster'. Phylogenetic analysis indicates that *Y. littoralis* represents the sister taxon of this 'eugaleaspid cluster'', and thus a new family of Eugaleaspidiformes, the Yongdongaspidae fam. nov., is erected. The genus *Yongdongaspis* as a plesiomorphic taxon relative to the 'eugaleaspid cluster' provides additional evidence for the subdivision and correlation of the URBs in South China.

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