第53卷 第2期
2015年4月

古 脊 椎 动 物 学 报
VERTEBRATA PALASIATICA

pp. 93-109
figs. 1-10

A streamlined jawless fish (Galeapida) from the Lower Devonian of Yunnan, China and its taxonomic and paleoecological implications

GAI Zhi-Kun ZHU Min* JIA Lian-Tao ZHAO Wen-Jin

(*Key Laboratory of Vertebrate Evolution and Human Origins of Chinese Academy of Sciences*, *Institute of Vertebrate Paleontology and Paleoanthropology*, *Chinese Academy of Sciences* Beijing 100044
* Corresponding author: zhumin@ivpp.ac.cn)

Abstract A new genus and species of the Huananaspiformes (Galeaspida), *Rhegmaspis xiphoidea*, is described from the Posongchong Formation (Pragian, Early Devonian), Zhaotong, Yunnan Province, China. The new taxon is characterized by having a torpedo-shaped head-shield, a long rostral process, ventrolaterally set orbits, and ventrally curved branchial fossae, but no corners, inner corners, and ventral rim of head-shield. It is assigned to the family Gantarostrataspidae that include *Gantarostrataspis* and *Wumengshanaspis*. According to the new material and new observation, the Gantarostrataspidae is emended and a fresh look is prososed for *Gantarostrataspis* and *Wumengshanaspis*. As a streamlined jawless fish, *Rhegmaspis* displays an adaptation for a suprabenthic lifestyle with more active feeding behavior among galeaspids. The new form not only enriches the diversity of the Huananaspiformes, but also provides evidence for the last adaptive radiation of galeaspids by occupying an unexploited ecological niche during the Pragian of the Early Devonian.

Key words Zhaotong, Yunnan; Lower Devonian; Galeaspida, Huananaspiformes; taxonomy; paleoecology

1 Introduction

The Galeaspida is a clade of fossil, armored jawless vertebrates, or “ostracoderms”, known from the Telychian (Llandovery, Silurian) to the Late Devonian (Gai et al., 2005, 2011; Janvier, 1996; Zhao and Zhu, 2010, 2014; Zhu and Gai, 2006; Zhu et al., 2015). Among jawless vertebrates, galeaspids are characterized by the festooned pattern of sensory canals on the dorsal side of head-shield, and a large median dorsal opening that serves as the main water intake device and the common nostril for separated nasal sacs and hypophysial duct (Gai and Zhu, 2012; Gai et al., 2011; Wang, 1991; Zhu et al., 2015).

Most galeaspids have a strongly flattened head-shield, dorsally set eyes, and a ventral mouth, indicating a benthic lifestyle moving on sandy or muddy substrates in coastal, marine environment (Janvier, 1996). Here, we describe a new galeaspid from the Lower Devonian

国家重点基础研究发展计划项目(编号：2012CB821902)、国家自然科学基金(批准号：41202015)、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)(编号：123101)资助。
收稿日期：2014-11-13

Posongchong Formation of Zhaotong, Yunnan Province, China (Fig. 1). The new form has a torpedo-shaped head-shield, a long rostral process and ventrolaterally set eyes, which highlight an adaptation to an active suprabenthic lifestyle.

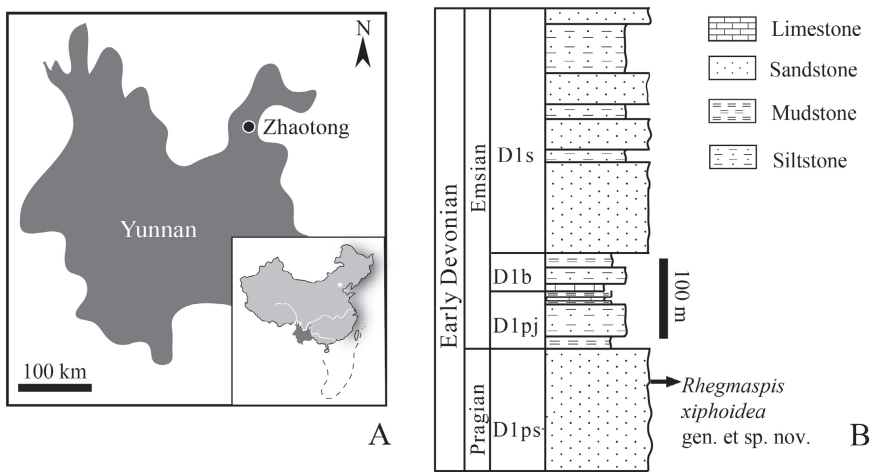

Fig. 1 Location map (A) and lithocolumn (B) of *Rhegmaspis xiphoidea* gen. et sp. nov. Abbreviations: D_{1s}. Suotoushan Formation; D_{1b}. Bianqinggou Formation; D_{1pj}. Pojiao Formation; D_{1ps}. Posongchong Formation

2 Materials and methods

The new material was collected from a yellow sandstone layer of the Posongchong Formation (Pragian, Lower Devonian), near the dam of the Qingmen Reservoir in the suburb of Zhaotong, northeastern Yunnan, South China (Liao et al., 1978; Lu et al., 2012) (Fig. 1). In addition to early vascular plants (e.g. *Catenalis digitata*, cover image, Hao and Xue, 2013: fig. 4.1), the Posongchong Formation yields abundant vertebrate fossils including galeaspids (Liu, 1975; Pan and Wang, 1981; Wang et al., 1996; Wang and Zhu, 1994), petalichthyids (Ji and Pan, 1999), arthrodires (Dupret, 2008), antiarchs (Wang et al., 1996), and sarcopterygians (Lu and Zhu, 2008, 2010; Lu et al., 2012; Zhu and Janvier, 1994; Zhu et al., 2012). The vertebrate faunal members are assigned to the *Sanchaspis-Asiaspis* assemblage (Macrovertebrate assemblage III) (Zhu et al., 2000) or the Xujiachong assemblage (Zhao and Zhu, 2010). The strata bearing the Xujiachong assemblage also include the Posongchong Formation in Wenshan, Yunnan, the Xujiachong Formation in Qujing, Yunnan, the Nagaoling Formation in Liujing, Guangxi, and the Pingyipu Group in Jiangyou, Sichuan (Zhao and Zhu, 2010; Zhu et al., 2000).

All fossils are housed at the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Chinese Academy of Sciences, Beijing. The specimens were prepared mechanically at IVPP using pneumatic air scribes and needles under microscopes.

3 Systematic paleontology

Subclass Galeaspida Tarlo, 1967

Supraorder Polybranchiaspidida Janvier, 1996

Order Huananaspiformes Janvier, 1975

Family Gantarostrataspidae Wang & Wang, 1992

Diagnosis (emended) Small- to medium-sized huananaspiforms; head-shield torpedo-shaped with subparallel lateral margins; no ventral rim of head-shield; long rostral process, bearing tiny spines occasionally; corner and inner corner absent; median dorsal opening oval in outline with long axis aligned with the rostro-caudal axis; pineal fossa small, leveled immediately behind orbital openings; orbits laterally or ventrolaterally placed; posterior supraorbital canals of both sides V-shaped, meeting posteriorly just behind pineal fossa; lateral transverse canals over 3 pairs; branchial fossae over 10 pairs; dorsal part of the branchial fossae curving ventrally.

Genus *Rhegmaspis* gen. nov.

Type species *Rhegmaspis xiphoidea* sp. nov.

Etymology *Rhegma*, Greek, rupture, breach; aspis Greek, shield.

Diagnosis Small-sized gantarostrataspid; torpedo-shaped head-shield with subparallel lateral margins; ventral rim of head-shield absent; rostral process long and slender; small orbits situated ventrolaterally in the head-shield and directed slightly downwards; sensory canal system with V-shaped posterior supraorbital canals; 12−16 pairs of branchial fossae; dorsal part of the branchial fossae curving ventrally; oralobranchial fenestra long fusiform in outline; ornaments comprising relatively large pentagonal, flat-topping tubercles.

Remarks *Rhegmaspis* can be referred to the family Gantarostrataspidae by its diagnostic torpedo-shaped head-shield with subparallel lateral margins, a long rostral process, and a large medial dorsal opening (Zhu and Gai, 2006). When compared with *Wumengshanaspis* and *Gantarostrataspis*, the new genus *Rhegmaspis* more resembles *Gantarostrataspis* in the outline of the median dorsal opening that is oval in shape with the long axis aligned with the rostro-caudal axis and with a slightly pointed rostral end. *Rhegmaspis* differs from *Gantarostrataspis* by its overall shape and size of the head-shield, slender rostral process bearing no tiny spines, ventrolaterally placed orbital opening, and probably less developed sensory canals. Besides, the ornaments of *Rhegmaspis* are relatively large pentagonal, flat-topping tubercles, which are distinct from evenly-distributed, minute round-topping tubercles of *Gantarostrataspis*. *Rhegmaspis* is more comparable to *Wumengshanaspis* than *Gantarostrataspis* in the overall outline and size of head-shield, slender rostral process, and ventrolaterally placed orbital openings. *Rhegmaspis* differs from *Wumengshanaspis* in smaller median dorsal opening, and more branchial fossae. In addition, the ornaments of *Wumengshanaspis* consist of fairly large round tubercles.

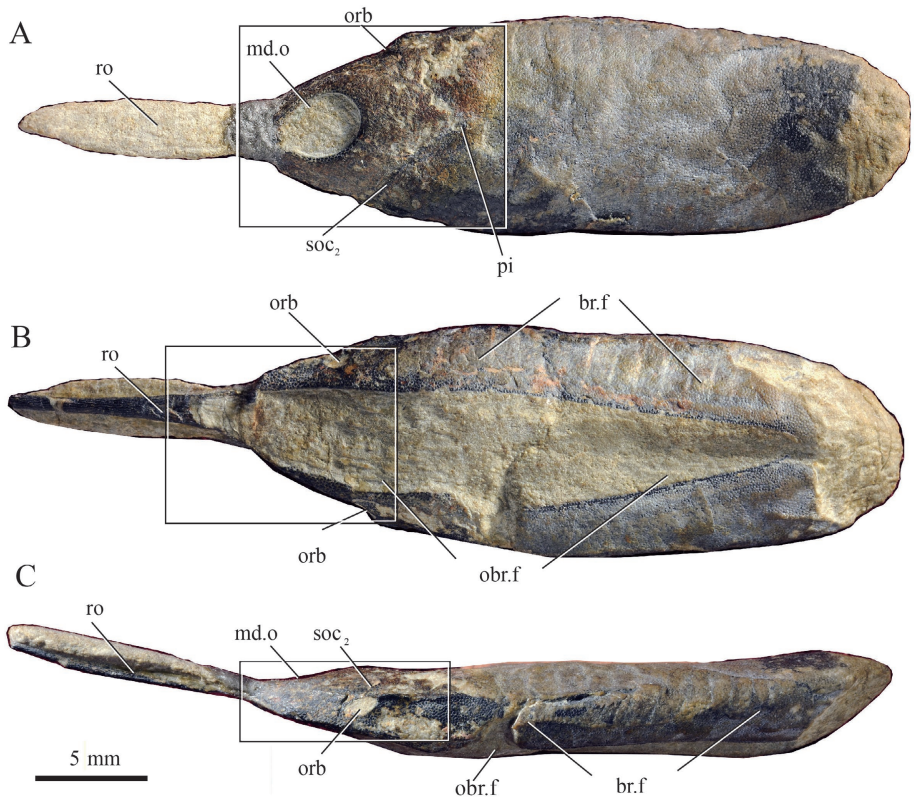

Fig. 2 Photograph of a complete head-shield of *Rhegmaspis xiphoidea* gen. et sp. nov. (IVPP V 19354.1A, holotype)
A. dorsal view, B. ventral view, C. lateral view
Abbreviations: br.f. branchial fossa 鳃穴; md.o. median dorsal opening 中背孔; obr.f. oralobrachial fenestra 口鳃窗; orb. orbital opening 眶孔; pi. pineal fossa 松果凹; ro. rostral process 吻突; soc_2. posterior supraorbital canal 后眶上管

***Rhegmaspis xiphoidea* sp. nov.**

(Figs. 2−6, 9E, 10B, cover image)

Etymology Xiphoideus (swordlike).

Holotype A complete head-shield (IVPP V 19354.1A, B).

Paratype A nearly complete head-shield (IVPP V 19354.2), an incomplete head-shield (V 19354.4), an incomplete endocast of skull (V 19354.3).

Horizon and type locality Early Devonian, Pragian, Posongchong Formation, Zhaotong, Yunnan, China.

Diagnosis As for type and only known species.

Measurements See Table1.

Description External morphology The new species is a small sized huananaspiform with a torpedo-shaped head-shield that has a long rostral process and subparallel lateral margins, and lacks a ventral rim. The holotype (IVPP V 19354.1A) is a three-dimensionally preserved head-shield (Figs. 2, 3), which has its maximum length of 35.90 mm (including the

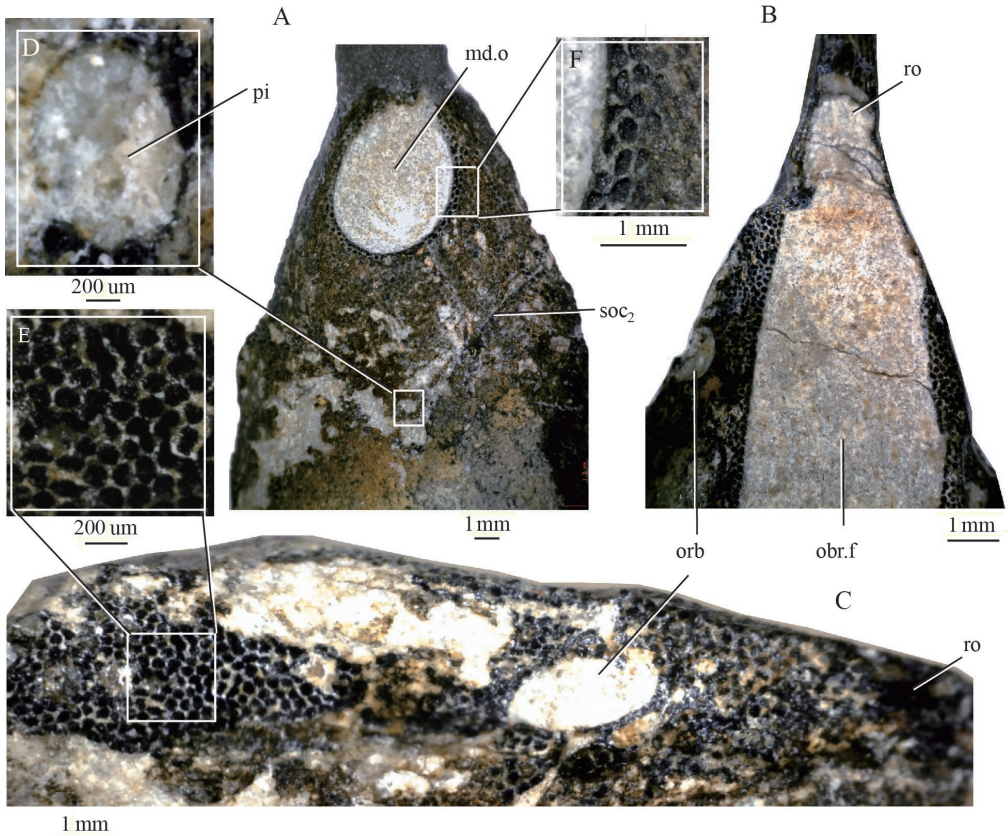

Fig. 3 Close-up of *Rhegmaspis xiphoidea* gen. et sp. nov. (IVPP V 19354.1A, holotype)
A−C. close-up of the anterior part of head-shield (box region of Fig. 2A−C): A. dorsal view; B. ventral view; C. lateral view; D. close-up of the pineal fossa; E. close-up of polygonal tubercles (box region of Fig. 3C); F. close-up of polygonal tubercles around the median dorsal opening, which form a dermal ring encircling the median dorsal opening. Abbreviations as in Fig. 2

Table 1 Measurements of *Rhegmaspis xiphoidea* gen. et sp. nov. (mm)

	IVPP V 19354.1	V 19354.2
Maximum length of head-shield	35.90	27.60
Maximum width of head-shield	9.50	12.13
Maximum height of head-shield	4.07	5.38
Diameter of orbital opening	1.48	1.53
Distance between orbital openings	5.95	6.50
Long axis of median dorsal opening	3.33	4.08
Short axis of median dorsal opening	2.55	3.39
Long axis of pineal fossa	0.49	_
Short axis of pineal fossa	0.34	_
Length of pre-pineal region	17.80	_
Length of post-pineal region	17.87	_
Length of rostral process	10.99	_
Maximum length of oralobranchial fenestra	24.09	25.50
Maximum width of oralobranchial fenestra	4.86	6.72

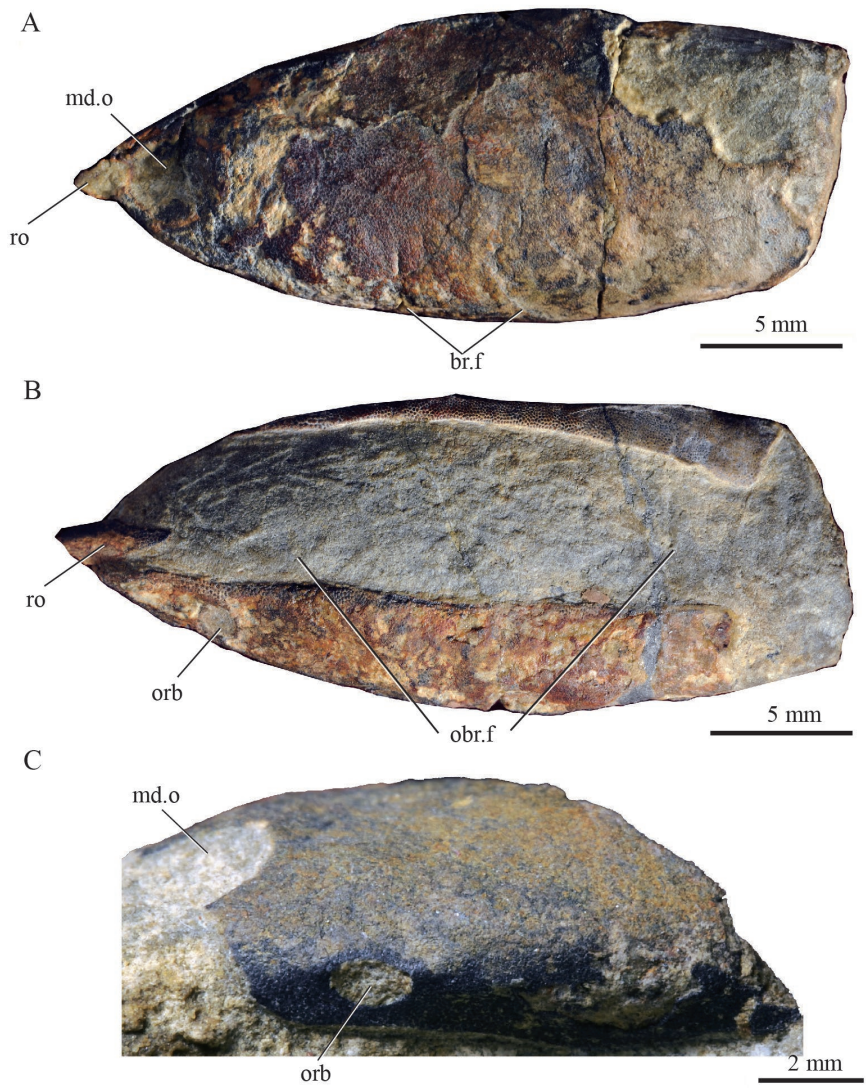

Fig. 4 Photograph of *Rhegmaspis xiphoidea* gen. et sp. nov.
A, B. a nearly complete head-shield, paratype, IVPP V 19354.2: A. dorasl view, B. ventral view;
C. an incomplete head-shield, paratype, V 19354.4, lateral view. Abbreviations as in Fig. 2

rostral process), the maximum breadth of 9.5 mm, and the maximum height of 4.07 mm. The head-shield approaches that of *Wumengshanaspis cuntianensis* (Wang and Lan, 1984) in size (Fig. 8A−C), but is much smaller than that of *Gantarostrataspis gengi* (Wang and Wang, 1992) (Fig. 7A−C). Rostrally, the head-shield protrudes into a long and slender rostral process. The preserved length of the rostral process of the holotype is about 10.99 mm (Table 1), and the estimated total length is about 13 mm (Fig. 5A−C). Caudally, the head-shield lacks any corner or inner corner. The median dorsal opening (md.o, Figs. 2−5) is fairly large and elliptic in outline with long axis aligned with the rostro-caudal axis. In the holotype, the long axis of the

median dorsal opening is 3.33 mm, and the short axis is 2.55 mm (Table 1). The length ratio of long axis and short axis of the median dorsal opening is about 1.306. The median dorsal opening extends posteriorly beyond the anterior level of orbits, but not beyond the posterior level of orbits. The three three-dimensionally preserved specimens show that the orbits have a more ventrolateral position on the head-shield (orb, Figs. 2−5). This is somewhat different from the lateral position of orbits in other huananaspiforms. The orbits are relatively small, round with the diameter range from 1.48 to 1.64 mm in three specimens (Table 1). In the holotype, the distance between two orbital openings is 5.95 mm. A tiny pineal fossa is located immediately behind the median dorsal opening in the midline (pi, Figs. 2A, 3A, D, 5A, C). The pineal fossa of the holotype is oval in outline with the long axis of 0.49 mm, and the short axis of 0.34 mm (Table 1). The lengths of pre- and post-pineal regions are 17.80 and 17.87 mm.

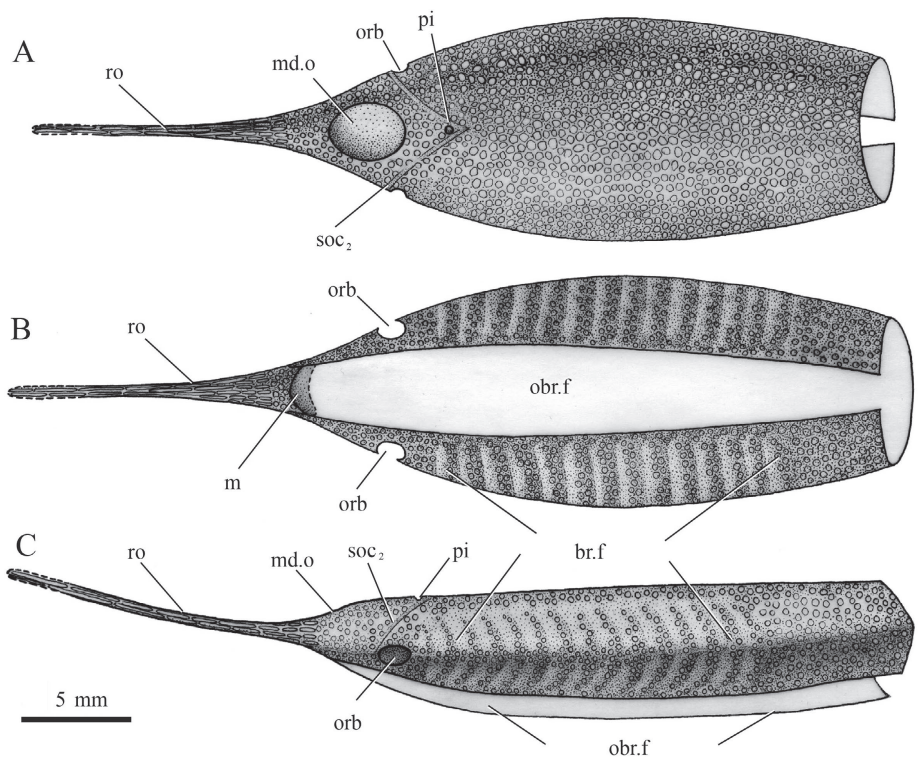

Fig. 5 Restoration of *Rhegmaspis xiphoidea* gen. et sp. nov.
A. dorsal view; B. ventral view; C. lateral view. Abbreviation: m. mouth, other abbreviations as in Fig. 2

Sensory canals are not preserved except the posterior supraorbital canals in holotype (soc_2, Figs. 2A, C, 3A, 5A, C). The paired posterior supraorbital canals (soc_2) are V-shaped and meet each other just posterior to the pineal fossa.

Different from most of other galeaspids, the new form is deficient of a ham-brim-like ventral rim. The dorsal part of head-shield curves ventrally to wrap a large oralobranchial chamber. The oralobranchial chamber opens to outside by a large oralobranchial fenestra (obr.f,

Figs. 2B, C, 3B, 4B, 5B, C), but it remains unknown whether there is a dermal plate covering the oralobranchial fenestra. The oralobranchial fenestra is long spindle-shaped, like a long rupture penetrating the ventral side of head-shield. The maximum length of the oralobranchial fenestra is 24.09 mm in the holotype, and 25.50 mm in the paratype (IVPP V 19354.2). The maximum width of the oralobranchial fenestra is 4.86 mm in the holotype, and 6.72 mm in the paratype (V 19354.2) (Table 1). No corresponding branchial opening is found along the lateral margins of the oralobranchial fenestra.

The entire exoskeletal head-shield is ornamented with relatively large pentagonal, flat-topping tubercles of variable size (Fig. 3C, E, F). The largest tubercles are located near the midline on the dorsal surface (about 65 tubercles/mm^2) and the smallest ones lie on the ventral side of the head-shield (75 tubercles /mm^2). The tubercles around the median dorsal opening form a dermal ring (Fig. 3A, F).

Internal anatomy The specimen IVPP V 19354.3 exhibits some cranial structures, e.g. the brain cavity, labyrinth cavities, cranial vascular canals, and branchial fossae (Fig. 6A, B), which were filled with mineral sediments to form a natural cast during the taphonomic process.

The natural cast of the brain cavity in V 19354.3 shows a series of swellings that probably correspond to the different divisions of the brain. From rostral to caudal, a faint swelling between the orbits probably stands for the mesencephalic division (mes, Fig. 6A−C), whereas a pair of bulbs between the anterior semicircular canals probably stand for the metencephalic division (met, Fig. 6A−C) and an elongate constriction between the labyrinth cavities for the myelencephalic division (mye, Fig. 6A−C). The myelencephalic division tapers posteriorly into a round canal that stands for the neural canal (nc, Fig. 6A−C).

On the side left to the brain cavity, the natural cast of the labyrinth cavity reveals the morphology of the inner ear. In dorsal view, two vertical semi-circular canals constitute distinct loops (asc, psc, Fig. 6A−C), curve ventro-medially to form two large bulging chambers that represent the anterior and posterior ampullae (aa, pa, Fig. 6A−C), and meet medially to form a vertical tube for the crus commissure (com, Fig. 6A−C).

Lateral to the labyrinth cavity, an elongate canal for the dorsal jugular vein, or lateral head vein (vcl, Fig. 6A−C), is set along the mesial margin of the branchial fossae. Anterolaterally, this canal expands in the orbital cavity, where a large venous sinus is assumed to be present. At the level of the labyrinth cavity, the canal curves to embrace the two vertical semicircular canals laterally.

The endoskeletal roof of the oralobranchial chamber in the holotype IVPP V 19534.1 and V 19534.3 reveals at least 12 pairs of branchial fossae (br.f, Figs. 2B, C, 4A, 5B, C, 6A−C). In *W. cuntianensis*, there are only 9 pairs of branchial fossae (br.f, Fig. 8A). The branchial fossae are separated transversely by the branchial arches (br.a, Fig. 6A, B). Noteworthy is that the ventrally curved branchial fossae render their impressions visible in lateral and ventral views of head-shield. This condition is exceptional for galeaspids, but probably also applies to *Wumengshanaspis*, *Gantarostrataspis*, and even *Sanqiaspis*, whose head-shields have

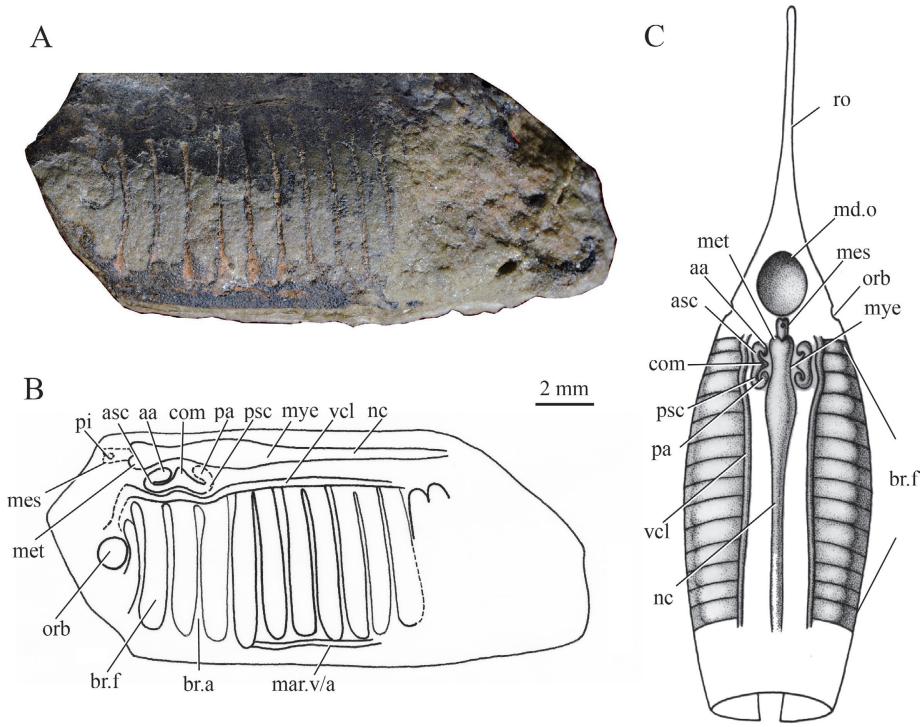

Fig. 6 Photograph (A), line drawing (B), and restoration (C) of the endocranium of *Rhegmaspis xiphoidea* gen. et sp. nov. (IVPP V 19354.3)

A, B. lateral view; C. dorsal view. Abbreviations: aa. anterior ampulla 前壶腹; asc. anterior semicircular canal 前半规管; br.a. branchial arch 鳃弓; com. commissural division of two vertical semicircular canals 前后半规管联合部; mar.v/a. marginal vein or artery 边缘静脉或动脉; mes. mesencephalic division 中脑区; met. metencephalic division 后脑区; mye. myelencephalic division 延脑区; nc. neural canal 神经管; pa. posterior ampulla 后壶腹; psc. posterior semicircular canals 后半规管; vcl. lateral head vein or dorsal jugular vein 头侧静脉或颈背静脉; other abbreviations as in Fig. 2

subparallel lateral margins. The branchial fossae in V 19354.3 were distorted and flattened to one plane (Fig. 6A, B). Along their lateral margin there exists a segment of canal that probably stands for the marginal vein or artery (mar.v/a, Fig. 6A−C) flanking the branchial fossae. The canal for marginal vein that is only identified in galeaspids and osteostracans, is difficult to be compared with the known veins in other Craniata (Janvier, 1981).

Gantarostrataspis Wang & Wang, 1992

(Figs. 7A−C, 9C)

Type species *Gantarostrataspis gengi* Wang & Wang, 1992.

Diagnosis (emended) A bowling-ball-shaped head-shield with a duck-billed rostral process; corner and inner corner absent; no ventral rim of head-shield; sensory canals developed; infraorbital canal forming a right angle with lateral dorsal canal; 3 pairs of lateral transverse canals issued from the infraorbital canal; at least 3 pairs of lateral transverse canals (probably 4 pairs) issued from the lateral dorsal canal; median transverse sensory canal short

and uniting the lateral dorsal canals anterior to the first lateral transverse sensory canal; dorsal commissure absent; V-shaped posterior supraorbital canals not convergent caudally, but connecting with the yoke-shaped median transverse sensory canal; more than 10 pairs of branchial fossae, probably curving ventrally; ornamentation consisting of small round tubercles.

Horizon and locality Posongchong Formation (Pragian, Lower Devonian), Gumu, Wenshan, Yunnan; Xujiachong Formation (Pragian, Lower Devonian), Xujiachong, Qujing, Yunnan (Zhu et al., 1994).

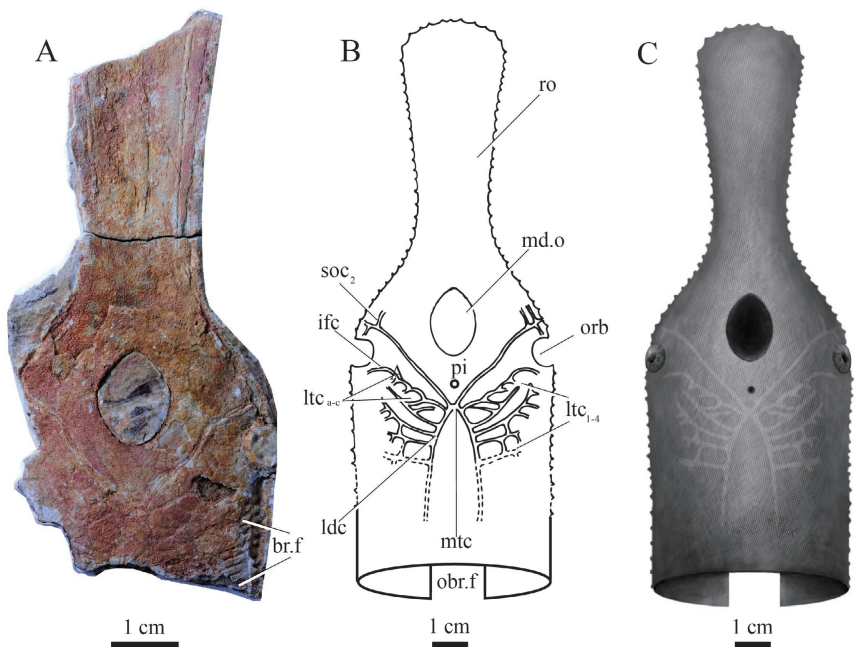

Fig. 7 Photograph (A), line drawing (B), and restoration (C) of *Gantarostrataspis gengi* (IVPP V 9758), in dorsal views (Modified from Wang and Wang, 1992; Liu et al., 2014)
Abbreviations: ifc. infraorbital canal 眶下管; ldc. lateral dorsal canal 侧背管; ltc_{1-4}. four lateral transverse canals issuing from the lateral dorsal canal 从侧背管发出的4条侧横管; ltc_{a-c}. three lateral transverse canals issuing from the infraorbital canal 从眶下管发出的3条侧横管; mtc. medial transverse canal 中横联络管; other abbreviations as in Fig. 2

Remarks The holotype of *G. gengi* missed the rear part of head-shield, and its initial restoration (Wang and Wang, 1992: fig. 1) was mainly based on *Sanqiaspis* that bears posteriorly projecting corner and inner corner (Fig. 9F). Liu et al. (2014) suggested that the head-shield of *Gantarostrataspis gengi* should be longer than previously restored because of the fourth pair of the lateral transverse canals probably on the rear part of the head-shield. By reference to *Rhegmaspis*, *Gantarostrataspis* probably lacks the posteriorly projecting corner and inner corner. A hat-brim-like ventral rim is also absent judging from the branchial fossae close the lateral margin of head-shield. The emendation of the sensory canal system is mainly based on the updated interpretation on the homology of its canals (Liu et al., 2014).

Wumengshanaspis Wang & Lan, 1984

(Figs. 8A–C, 9D)

Type species *Wumengshanaspis cuntianensis* Wang & Lan, 1984.

Diagnosis (emended) A torpedo-shaped head-shield with a long rostral process; corner and inner corner absent; no ventral rim of head-shield; median dorsal opening oval in shape, large but not beyond the posterior margin of the orbital openings; ornamentation consisting of relative large round tubercles.

Horizon and locality Lower part of the Suotoushan Formation (Lower to Middle Devonian); Yiliang, Yunnan.

Remarks The corner and inner corner of *Wumengshanaspis* were previously restored to be present like *Sanqiaspis* (Wang and Lan, 1984). In addition, the median dorsal opening was restored to extend posteriorly beyond the level of the first branchial fossa. The reexamination of the holotype (IGCAGS V 1744.1) (Fig. 8A) suggests that both corner and inner corner, as well as the ventral rim of head-shield, are absent. The median dorsal opening is much smaller than initially restored. The serrated spines on rostral process are probably relatively large tubercles of the ornamentation.

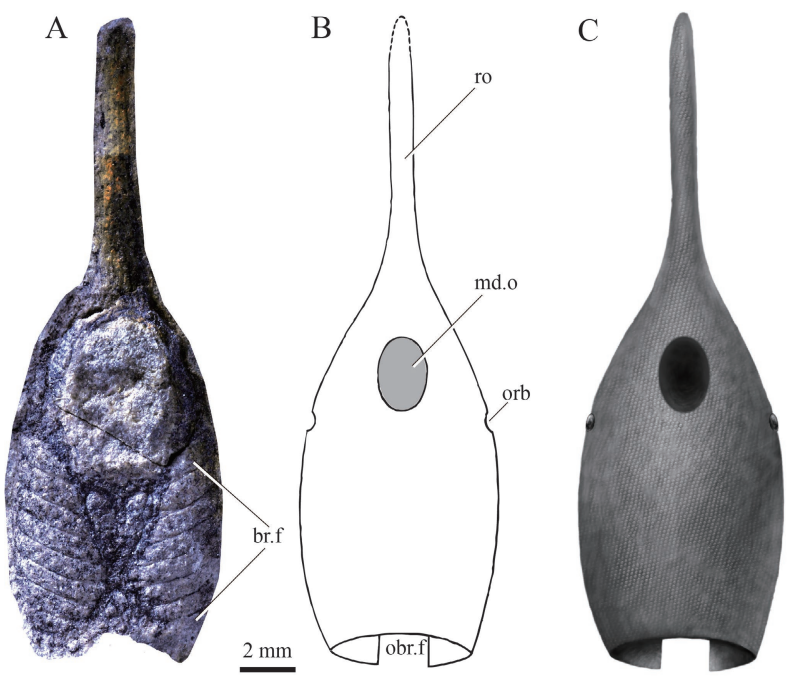

Fig. 8 Photograph (A), line drawing (B), and restoration (C) of *Wumengshanaspis cuntianensis* (IGCAGS V 1744.1), dorsal views (Modified from Wang and Lan, 1984)
Abbreviations as in Fig. 2

4 Discussion

4.1 Taxonomic implications

The Gantarostrataspidae was erected based on the type genus *Gantarostrataspis* (Wang and Wang, 1992), and currently comprises three genera *Gantarostrataspis*, *Wumengshanaspis*, and *Rhegmaspis*. *Wumengshanaspis* was originally referred to the Huananaspidae by Wang and Lan (1984), but all members of the Huananaspidae have a pair of laterally projecting corners (Gai and Zhu, 2007). Zhu and Gai (2006) suggested that *Wumengshanaspis* and *Gantarostrataspis* probably formed a monophyletic group based on the synapomorphies such as the subparallel lateral margins of head-shield, large median dorsal opening, spiny rostral process, and posteriorly projecting corners. Thus, *Wumengshanaspis* was referred to the Gantarostrataspidae in the first cladistically-based classification of the Galeaspida (Zhu and Gai 2006; Zhu et al., 2015). It is noteworthy that the restored corners in *Gantarostrataspis* and *Wumengshanaspis* were inferred from the condition in the Sanqiaspidae (Fig. 9F), a family closely allied to the Gantarostrataspidae (Fig. 9C−E). The discovery of *Rhegmaspis* highlights that the 'so-called' posteriorly projecting corners are probably not existent in *Wumengshanaspis* and *Gantarostrataspis*. Among galeaspids, the absence of corner and inner corner is also seen in the Duyunolepidae such as *Duyunolepis* (Halstead, 1979; P'an and Wang, 1978; Pan and

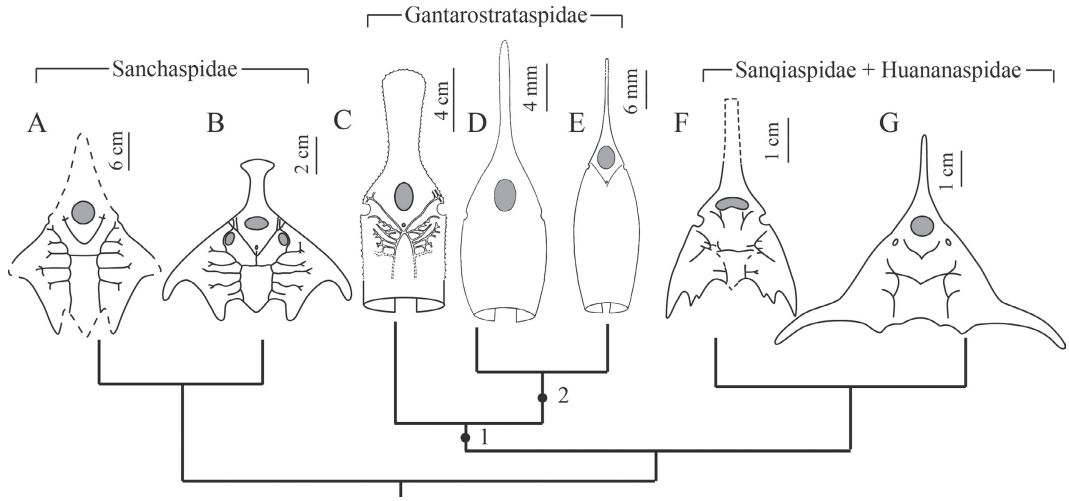

Fig. 9 Phylogenetic relationships of the Huananaspiformes (after tree topology in Zhu and Gai, 2006), with particular reference to the most inclusive taxa of the clade

A−H. Head-shields of huananaspiforms, dorsal views: A. *Antiquisagittaspis* (redrawn after Liu, 1985); B. *Sanchaspis* (redrawn after Pan and Wang, 1981); C. *Gantarostrataspis* (redrawn after Wang and Wang, 1992); D. *Wumengshanaspis* (redrawn after Wang and Lan, 1984); E. *Rhegmaspis*; F. *Sanqiaspis* (redrawn after Liu, 1975; Wang et al., 1996); G. *Asiaspis* and all other Huananaspiformes (redrawn after P'an et al., 1975); Node 1. Gantarostrataspidae defined by synapomorphies: subparallel lateral margins of head-shield, ventrally curved branchial fossae, and absence of corner, inner corner, and ventral rim of head-shield; Node 2. (*Wumengshanaspis* + *Rhegmaspis*) defined by synapomorphies: a torpedo-shaped head-shield, slender rostral process, and ventrolaterally placed orbital openings

Wang, 1982), *Paraduyunaspis* (P'an and Wang, 1978), and *Lopadaspis* (Wang et al., 2001). However, the Duyunolepidae more resembles the Polybranchiaspidae in other characters such as oval-like head-shield, dorsally-positioned orbital opening, and absence of rostral process. Zhu (1992) suggested that the so-called corner of polybranchiaspids should be homologous to the inner corner of huananaspids and eugaleaspids. Thus, the Duyunolepidae is regarded as a specialized subgroup of the Polybranchiaspiformes by the burst of branchial fossae (more than 20 pairs), and the absence of inner corners (Liu, 1993; Zhu and Gai, 2006). In *Rhegmaspis*, *Wumengshanaspis*, and probably *Gantarostrataspis*, the head-shield is largely narrowed and thickened to form a torpedo-shaped head-shield by curving transversely elongated branchial fossae ventrally. This evolutionary change probably resulted in the absence of ham-brim-like ventral rim of head-shield, and the ventrolaterally set orbits. It might also have a connection with the absence of the corner and inner corner. Therefore, the synapomorphies defining the Gantarostrataspidae can be emended as subparallel lateral margins of head-shield, ventrally curved branchial fossae, and absence of corner, inner corner, and ventral rim of head-shield (Fig. 9, Node 1).

4.2 Paleoecological implications

The highly peculiar shape of the head-shield of *Rhegmaspis* probably reflects a different lifestyle from other galeaspids. Generally, most of galeaspids have a strongly flattened head-shield, dorsally-positioned eyes and 'nostril', and a ventral mouth that opens downward. Their overall body shape of a flattened heavy head-shield and a narrow, tapering body (as seen that of '*Dongfangaspis*' *qujingensis* Pan, 1992: fig. 12) may help them remain on the bottom in moderate currents without a significant energetic cost (Fig. 10A), which are functionally analogous to many other benthic living fishes such as angel sharks, skates, rays, squarehead catfishes, ogcocephalid batfishes, platycephalid flatheads, and some scorpion fishes (Helfman et al., 2009). The positions of mouth and eyes in living fishes also correlate with their habitat and feeding. Fishes that feed on benthic food types normally have subterminal or inferior mouth that allows to filter small organisms from bottom sediments while swimming, whereas their eyes set close together on the top of the head, which are well suited for detecting above dangers in the water (Helfman et al., 2009). The morphological adaptations of galeaspids indicate that they are bottom-dwellers living in a benthic habitat on sandy or muddy substrates in marginal, marine environment (Janvier, 1996).

Compared to common galeaspids, *Rhegmaspis* had a unique shape of head-shield for effective swimming. The materials of *Rhegmaspis* indicate that the small fish had evolved a torpedo-shaped head-shield which was largely narrowed and thickened by curving the transversely elongated branchial fossae ventrally and discarding the ham-like ventral rim (Fig. 10A_2, B_2). The torpedo-shaped head-shield displayed much better streamlining body than the strongly flattened head-shield. This shape can minimize water drag by reducing the magnitude of the pressure gradient over the body allowing water to flow over the surface without

separation (Vogel, 1994) (Fig. 10A_1, B_1). Meanwhile, *Rhegmaspis* is hardly to be a bottom-dweller as it had developed a long rostral, presumably stabilizing or stirring, projection, and ventrolaterally set orbits. These adaptions all suggest the small fish probably had obtained considerable maneuverability for an apparently suprabenthic existence (Helfman et al., 2009). Lived in a suprabenthic habitat, *Rhegmaspis* probably had a more active feeding behavior, e.g., it may use the long rostral process as a scraper to plow the bottom in a relative high speed, and the ventrolaterally set eyes to prey detection for stirred digestible materials simultaneously so that the ventral mouth can pump and filter them more effectively than that of benthic galeaspids.

The morphological adaption of *Rhegmaspis* indicates a strong selection for increased mobility and maneuverability during the Pragian of the Early Devonian. The galeaspids in the Posongchong Formation show a high diversity that includes *Kwangnanaspis subtriangularis* (Cao, 1979), *Sanqiaspis zhaotongensis* (Liu, 1975; Wang et al., 1996), *S. rostrata* (Zhao et al., 2002), *Gantarostrataspis gengi* (Wang and Wang, 1992), *Gumuaspis rostrata* (Wang and Wang, 1992), *Macrothyraspis longicornis* (Zhao et al., 2002), *M. longilanceus* (Wang et al., 2005), *Qingmenaspis microculus* (Pan and Wang, 1981), *Zhaotongaspis janvieri* (Wang and Zhu, 1994), *Lungmenshanaspis yunnanensis* (Wang et al., 1996), and several undescribed new

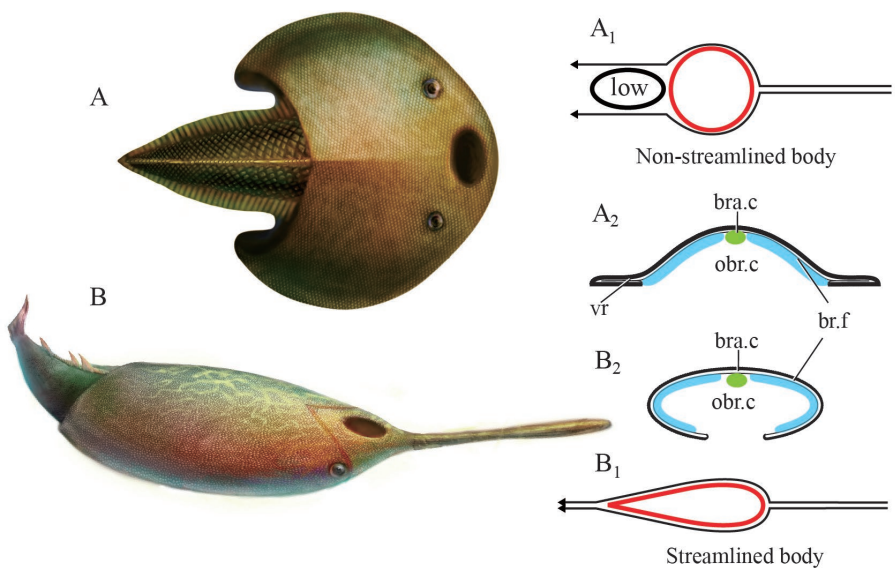

Fig. 10 The lifestyle of galeaspids in benthic (A) and superbenthic (B) habitats

A. '*Dongfangaspis*' *qujingensis* with a flattened head-shield, which is suggestive of a benthic habitat; A_1. a flattened head-shield bears much water pressure drag when swimming, but permit remaining on the bottom without a significant energetic cost; A_2. a cross section of the head-shield, showing the transversely elongated branchial fossae and ventral rim; B. *Rhegmaspis xiphoidea* with streamlined body, which is more suggestive of a superbenthic habitat; B_1. a streamlined body can minimize water pressure drag largely when swimming; B_2. a cross section of the head-shield, showing the ventrally curved branchial fossae and absence of ventral rim. Abbreviations: bra.c. brain cavity 脑腔; br.f. branchial fossae 鳃穴; obr.c. oralobrachial chamber口鳃室; vr. ventral rim 腹环

forms. Janvier (1996) thought that some huananaspiforms with the long and slender corner and rostral process, such as *Sanqiaspis* or *Lungmenshanaspis*, probably had a more active nektonic habitat as some boreaspid osteostracans. Given the success of flattened galeaspids in benthic habitat, it is not surprising that some galeaspids such as *Rhegmaspis* and *Sanqiaspis* had increased their aquatic behavior and swimming performance to occupy an unexploited ecological niche. This may explain why galeaspids, especially huananaspiforms, experienced a rapid radiation during the Pragian of the Early Devonian (Zhu and Gai, 2006; Zhu et al., 2015). After that, the diversity of galeaspids suddenly decreased, and few galeaspids survived into the Famennian of the Late Devonian (Pan et al., 1987).

Acknowledgments We thank Lu Jing, Qiao Tuo and Pan Zhaohui for their help in the fieldwork. We are grateful to professor Chang Meeman and Zhang Jiangyong for the improvement of manuscript, and Shi Aijuan and Yang Dinghua for drawing illustrations and ecological restoration.

云南早泥盆世一流线型盔甲鱼及其分类学与古生态学意义

盖志琨 朱 敏* 贾连涛 赵文金

(中国科学院脊椎动物演化与人类起源重点实验室，中国科学院古脊椎动物与古人类研究所 北京100044 *通讯作者)

摘要：记述了云南昭通早泥盆世布拉格期坡松冲组华南鱼目一新属、新种——剑裂甲鱼(*Rhegmaspis xiphoidea* gen. et sp. nov.)。新属的主要特征是：具有鱼雷形头甲，细长吻突，眶孔位于头甲腹侧位，鳃穴向头甲腹面弯曲，角、内角和腹环丢失。鉴于以上特征，新属被归到了包括鸭吻鱼和乌蒙山鱼在内的鸭吻鱼科。根据新材料提供的信息，修订了鸭吻鱼科，包括鸭吻鱼和乌蒙山鱼的鳃穴、腹环、角、内角等特征。裂甲鱼属是该地区发现的第一个具有流线形体型的盔甲鱼类，指示了该地区一些盔甲鱼类可能开始了一种营上底栖的生活方式，具有更加主动的取食行为。新属的发现不仅丰富了该地区华南鱼目的多样性，而且提供了盔甲鱼类在早泥盆世布拉格期通过占据新的生态位而发生的最后一次辐射演化的证据。

关键词：云南昭通，下泥盆统，盔甲鱼亚纲，华南鱼目，分类，古生态

中图法分类号: Q915.861 **文献标识码**: A **文章编号**: 1000-3118(2015)02-0093-17

References

Cao R G, 1979. A Lower Devonian agnathan of South-Eastern Yunnan. Vert PalAsiat, 17(2): 118−120

Dupret V, 2008. A new wuttagoonaspid (Placodermi, Arthrodira) from the Lower Devonian of Yunnan (South China): origin, dispersal, and paleobiogeographic significance. J Vert Paleont, 28(1): 12−20

Gai Z K, Zhu M, 2007. First discovery of Huananaspidae from the Xishancun Formation (Lochkovian, Devonian) of Yunnan, China. Vert PalAsiat, 45(1): 1−12

Gai Z K, Zhu M, 2012. The origin of the vertebrate jaw: intersection between developmental biology-based model and fossil evidence. Chin Sci Bull, 57(30): 3819−3828

Gai Z K, Zhu M, Zhao W J, 2005. New material of eugaleaspids from the Silurian of Changxing, Zhejiang, China, with a discussion on the eugaleaspid phylogeny. Vert PalAsiat, 43(1): 61−75

Gai Z K, Donoghue P C J, Zhu M et al., 2011. Fossil jawless fish from China foreshadows early jawed vertebrate anatomy. Nature, 476: 324−327

Halstead L B, 1979. Internal anatomy of the polybranchiaspids (Agnatha, Galeaspida). Nature, 282: 833−836

Hao S G, Xue J Z, 2013. The Early Devonian Posongchong Flora of Yunnan—A Contribution to an Understanding of the Evolution and Early Diversification of Vascular Plants. Beijing: Science Press. 1−366

Helfman G, Collette B B, Facey D E et al., 2009. The Diversity of Fishes: Biology, Evolution, and Ecology, 2nd ed. London: Wiley-Blackwell. 1−720

Janvier P, 1975. Anatomie et position systématique des Galéaspides (Vertebrata, Cyclostomata), Céphalaspidomorphes du Dévonien inférieur du Yunnan (Chine). Bull Mus Natl Hist Nat, Paris, 278: 1−16

Janvier P, 1981. The phylogeny of the Craniata, with particular reference to the significance of fossil “agnathans”. J Vert Paleont, 1(2): 121−159

Janvier P, 1996. Early Vertebrates. Oxford: Clarendon Press. 1−393

Ji S A, Pan J, 1999. New Devonian petalichthyids (Placodermi) from eastern Yunnan, China. Prof Pap Stratigr Palaeont, 27: 172−179

Liao W H, Xu H K, Wang C Y et al., 1978. The subdivision and correlation of the Devonian stratigrphy of south-west of China. In: Institute of Geology and Mineral Resources of the Chinese Academy of Geological Sciences ed. Symposium on the Devonian System of South China. Beijing: Geological Publishing House. 193–213

Liu Y H, 1975. Lower Devonian agnathans of Yunnan and Sichuan. Vert PalAsiat, 13(4): 202−216

Liu Y H, 1985. A galeaspid (Agnatha), *Antiquasagittaspis cornuta* gen. et sp. nov., from Lower Devonian of Guangxi, China. Vert PalAsiat, 23(4): 247−254

Liu Y H, 1993. Do the lateral fields exist in some galeaspids (jawless fishes)? Vert PalAsiat, 31(4): 315−324

Liu Y H, Gai Z K, Zhu M, 2014. The discussion on some problems in galeaspids (Agnatha). Vert PalAsiat, 52(4): 349−363

Lu J, Zhu M, 2008. An Early Devonian (Pragian) sarcopterygian from Zhaotong, Yunnan, China. Vert PalAsiat, 46(3): 161−170

Lu J, Zhu M, 2010. An onychodont fish (Osteichthyes, Sarcopterygii) from the Early Devonian of China, and the evolution of the Onychodontiformes. Proc R Soc B, 277: 293−299

Lu J, Zhu M, Long J A et al., 2012. The earliest known stem-tetrapod from the Lower Devonian of China. Nat Commun, 3: 1160

Pan J, 1992. New galeaspids (Agnatha) from the Silurian and Devonian of China. Beijing: Geological Publishing House. 1−77

Pan J, Wang S T, 1981. New discoveries of polybranchiaspids from Yunnan Province. Vert PalAsiat, 19(2): 113−121

Pan J, Wang S T, 1982. A nomenclatural note on *Duyunolepis* for *Duyunaspis* P’an et Wang, 1978. Vert PalAsiat, 20(4): 370

Pan J, Huo F C, Cao J X et al., 1987. Continental Devonian System of Ningxia and its Biotas. Beijing: Geological Publishing House. 1−237

P'an K, Wang S T, 1978. Devonian Agnatha and Pisces of South China. In: Institute of Geology and Mineral Resources of the Chinese Academy of Geological Sciences ed. Symposium of the Devonian System of South China. Beijing: Geological Publishing House. 299−333

P'an K, Wang S T, Liu Y P, 1975. The Lower Devonian Agnatha and Pisces from South China. Prof Pap Stratigr Paleont, 1: 135−169

Vogel S, 1994. Life in Moving Fluids. Princeton: Princeton University Press. 1−484

Wang J Q, Wang N Z, 1992. Early Devonian galeaspid Agnatha from southeast of Yunnan, China. Vert PalAsiat, 30(3): 185−194

Wang J Q, Zhu M, 1994. *Zhaotongaspis janvieri* gen. et sp. nov., a galeaspid from Early Devonian of Zhaotong, northeastern Yunnan. Vert PalAsiat, 32(4): 231−243

Wang J Q, Fan J H, Zhu M, 1996. Early vertebrate fossils from the Early Devonian of Zhaotong District, northeastern Yunnan. Vert PalAsiat, 34(1): 1−17

Wang J Q, Gai Z K, Zhu M, 2005. A new species of *Macrothyraspis* (Galeaspida, Agnatha) from Wenshan, Yunnan, China. Vert PalAsiat, 43(4): 304−311

Wang N Z, 1991. Two new Silurian galeaspids (jawless craniates) from Zhejiang Province, China, with a discussion of galeaspid-gnathostome relationships. In: Chang M M, Liu Y H, Zhang G R eds. Early Vertebrates and Related Problems of Evolutionary Biology. Beijing: Science Press. 41−66

Wang S T, Lan C H, 1984. New discovery of polybranchiaspids from Yiliang County, northeast Yunnan Province. Bull Geol Inst, 9: 113−120

Wang S T, Wang J Q, Wang N Z et al., 2001. A new genus of Galeaspida from the late Early Devonian of eastern Guangxi, South China. Vert PalAsiat, 39(3): 157−167

Zhao W J, Zhu M, 2010. Siluro-Devonian vertebrate biostratigraphy and biogeography of China. Palaeoworld, 19(1-2): 4−26

Zhao W J, Zhu M, 2014. A review of the Silurian fishes from China, with comments on the correlation of fish-bearing strata. Earth Sci Front, 21(2): 185−202

Zhao W J, Zhu M, Jia L T, 2002. New discovery of galeaspids from Early Devonian of Wenshan, southeastern Yunnan, China. Vert PalAsiat, 40(2): 97−113

Zhu M, 1992. Two new eugaleaspids, with a discussion on eugaleaspid phylogeny. Vert PalAsiat, 30(3): 169−184

Zhu M et al., 2015. Palaeovertebrata Sinica. Volume 1, Fishes. Fascicle 1 (Serial no. 1): Agnathans. Beijing: Science Press. 1−294

Zhu M, Gai Z K, 2006. Phylogenetic relationships of galeaspids (Agnatha). Vert PalAsiat, 44(1): 1−27

Zhu M, Janvier P, 1994. Un onychodontide (Vertebrata, Sarcopterygii) du Dévonien inférieur de Chine. C R Acad Sci Paris, Sér II, 319: 951−956

Zhu M, Wang J Q, Fan J H, 1994. Early Devonian fishes from Guijiatun and Xujiachong formations of Qujing, Yunnan, and related biostratigraphic problems. Vert PalAsiat, 32(1): 1−20

Zhu M, Wang N Z, Wang J Q, 2000. Devonian macro- and microvetebrate assemblages of China. Cour Forschungstinst Senckenb, 223: 361−372

Zhu M, Yu X B, Lu J et al., 2012. Earliest known coelacanth skull extends the range of anatomically modern coelacanths to the Early Devonian. Nat Commun, 3: 772