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

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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...
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.

![Location map (A) and lithocolumn (B) of *Rhegmaspis xiphoidea* gen. et sp. nov.](image)

**Fig. 1** Location map (A) and lithocolumn (B) of *Rhegmaspis xiphoidea* gen. et sp. nov.

Abbreviations: D₁s, Suotoushan Formation; D₁b, Bianqinggou Formation; D₁pj, Pojiao Formation; D₁ps, 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 鰓穴; md.o. median dorsal opening 中背孔; obr.f. oralobrachial fenestra 口鳃窗; orb. orbital opening 眼孔; pi. pineal fossa 松果凹; ro. rostral process 吻突; soc. 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 oralbranchial fenestra | 24.09   | 25.50           |
| Maximum width of oralbranchial fenestra | 4.86    | 6.72            |
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.

Sensory canals are not preserved except the posterior supraorbital canals in holotype (soc₂, Figs. 2A, C, 3A, 5A, C). The paired posterior supraorbital canals (soc₂) 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 oralbranchial chamber. The oralbranchial chamber opens to outside by a large oralbranchial 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, flattopping tubercles of variable size (Fig. 3C, E, F). The largest tubercles are located near the midline on the dorsal surface (about 65 tubercles/mm²) and the smallest ones lie on the ventral side of the head-shield (75 tubercles/mm²). 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 galeaspid, but probably also applies to *Wumengshanaspis, Gantarostrataspis*, and even *Sanqiaspis*, whose head-shields have
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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)


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).

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**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](image)

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, ogocepalid 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. 10A₂, B₂). 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, B). 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.

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 nektic 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).

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References


