New Discoveries of Galeaspids (Agnatha) from the Lower Devonian of Qujing, Yunnan, China (Postprint)

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Abstract

New findings of galeaspids (Agnatha) including Altigibbaspis huiqingae gen. et sp. nov., an indeterminate polybranchiaspid, Eugaleaspis changi, and Nanpanaspis microculus are described from the lower part of the Xishancun Formation (early Lochkovian, Early Devonian) near the northeast entrance of Liaokuo Park, Qujing City, Yunnan Province, China. The Polybranchiaspis-like new genus is characterized by a blade-like median dorsal ridge on the dorsal side of head-shield. The morphological disparity of the median dorsal ridge and spine in galeaspids suggests that these structures functioned more than providing a hydrodynamic stability. We assume that a high upright and compressed spine may render galeaspid fishes an apparently larger size as seen by a predator, and a blade-like median dorsal ridge may accomplish a defense against the claws of large sea scorpions. Nanpanaspis is peculiar in bearing two short laterally projecting processes on each side of the head-shield, and its phylogenetic relationship is discussed based on different interpretations on the homology of these processes. Considering the unique morphology of Nanpanaspis, and its early occurrence among the Huananaspiformes, we assign Nanpanaspis in the monogeneric family Nanpanaspidae to represent an early branch of the Huananaspiformes.

Full Text

Preamble

New Findings of Galeaspids (Agnatha) from the Lower Devonian of Qujing, Yunnan, China

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Abstract

New findings of galeaspids (Agnatha) from the lower part of the Xishancun Formation (early Lochkovian, Early Devonian) near the northeast entrance of Liaokuo Park, Qujing City, Yunnan Province, China, are described, including *Altigibbaspis huiqingae* gen. et sp. nov., an indeterminate polybranchiaspid, *Eugaleaspis changi*, and *Nanpanaspis microculus*. The Polybranchiaspis-like new genus is characterized by a blade-like median dorsal ridge on the dorsal side of the head-shield. The morphological disparity of the median dorsal ridge and spine in galeaspids suggests that these structures functioned for more than just providing hydrodynamic stability. We propose that a high, upright, and compressed spine may have rendered galeaspid fishes apparently larger in the eyes of predators, while a blade-like median dorsal ridge may have served as a defense against the claws of large sea scorpions. *Nanpanaspis* is peculiar in bearing two short, laterally projecting processes on each side of the head-shield, and its phylogenetic relationship is discussed based on different interpretations of the homology of these processes. Considering the unique morphology of *Nanpanaspis* and its early occurrence among the Huananaspiformes, we assign *Nanpanaspis* to the monogeneric family Nanpanaspidae to represent an early branch of the Huananaspiformes.

Key words: galeaspids, Lower Devonian, Qujing, Yunnan, China; Xishancun Formation

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1. Introduction

The Qujing District of Yunnan Province in South China preserves a succession of non-marine Lower Devonian strata [Figure 1: see original paper]A, which are subdivided in ascending order into the Xishancun, Xitun, Guijiatun, and Xujiachong formations [Figure 1: see original paper]B. The Devonian Xishancun Formation conformably overlies the Silurian Yulungssu Formation and is in turn conformably overlain by the Xitun Formation [Figure 1: see original paper]B (Zheng and Zhang, 1989; Dong, 1992; Zeng et al., 1992; Fan and Liu, 1995; Shan and Wang, 2000). The Xishancun Formation consists mainly of gray-yellow sandstone and siltstone intercalated with silty shale (Fang et al., 1985) and yields a diversified early vertebrate assemblage including galeaspids (Agnatha), placoderms, and sarcopterygians (Liu, 1965, 1975; P' an and Wang, 1978; Wang and Dong, 1989; Wang, 1995a, b; Wang, 2000; Zhu, 1992; Zhu and Schultze, 1997; Zhu et al., 1999; Gai and Zhu, 2007; Zhao and Zhu, 2010; Liu et al.,

2015; Si et al., 2015). To date, 12 genera and 17 species of galeaspids have been recorded from the Xishancun Formation (Liu et al., 2015; Si et al., 2015).

Here we describe new galeaspid materials including *Altigibbaspis huiqingae* gen. et sp. nov., an indeterminate polybranchiaspid, *Eugaleaspis changi*, and *Nanpanaspis microculus* from the lower part of the Xishancun Formation near the northeast entrance of Liaokuo Park in Qujing City [Figure 1: see original paper]C. The new materials were collected by the first author in the 1980s from a siltstone lenticle less than 1 m^2 in area and about 5 cm thick. The fish-bearing lenticle, embedded in a medium-thick layer of yellow sandstone, yielded mainly small galeaspid and placoderm fragments, indicating a heterochthonous burial. Notably, the type specimens of *E. changi* and *N. microculus* were erroneously reported as coming from the Xitun Formation in their original descriptions (Liu, 1965, 1975, 1979). In fact, all were excavated from the middle part of the Xishancun Formation together with *Szelepis yunnanensis* (Actinolepidae, Arthrodira) at another site on Liaokuoshan (formerly Liaojiaoshan, Liu, 1979).

[Figure 1: see original paper] Locality map and stratigraphic position of the fossil bed yielding *Altigibbaspis huiqingae* gen. et sp. nov. (Modified from Pan et al., 2015; Hao et al., 2007; Si et al., 2015)

2. Systematic Paleontology

Subclass Galeaspida Tarlo, 1967
Supraorder Polybranchiaspidida Janvier, 1996
Order Polybranchiaspiformes Liu, 1965
Family Polybranchiaspidae Liu, 1965
Genus *Altigibbaspis* gen. nov.

Etymology. The generic name derives from *alt* (L.), high; *gibb* (L.), hunchback; and *aspis* (Gr.), shield (commonly used as a suffix in generic names of Agnatha), referring to the hump-like profile of the head-shield bearing a robust and high median dorsal ridge.

Type species. *Altigibbaspis huiqingae* gen. et sp. nov.

Diagnosis. As for the type species.

Altigibbaspis huiqingae gen. et sp. nov. (Figs. 2–3)

Holotype. A nearly complete head-shield, IVPP V 20843.1 [Figure 2: see original paper]A–C.

Paratype. An incomplete head-shield, IVPP V 20843.2 [Figure 2: see original paper]D.

Etymology. The specific name honors the late Mrs. Hu Hui-Qing of IVPP, Chinese Academy of Sciences, for her contributions to exquisite illustrations of fossil vertebrates.

Locality and Horizon. Near the northeast entrance of Liaokuo Park, Qujing City, Yunnan Province, China; Xishancun Formation, Early Devonian (early Lochkovian).

Diagnosis. A medium-sized polybranchiaspid with a robust and high median dorsal ridge on the dorsal side of the head-shield; the posterior margin of the shield deeply embayed and bearing a dorsal spine in the middle; the inner corners extending backward well beyond the median dorsal spine; the lateral transverse canals not branching at their ends; the dorsal commissure situated anteriorly at the first two-fifths of the shield.

Remarks. The new genus *Altigibbaspis* closely resembles *Polybranchiaspis* in head-shield outline, relative position of the median dorsal and orbital openings, distribution pattern of sensory canals, and large ornamental tubercles. They differ in the extension of the inner corners, relative position of the dorsal commissure, and particularly in the development of the median dorsal ridge on the head-shield. In *Polybranchiaspis*, the inner corner is moderately developed with its posterior tip level with the end of the median dorsal spine, whereas in *Altigibbaspis* the inner corner is greatly developed, with its posterior tip extending well beyond the end of the median dorsal spine. The dorsal commissure is located in the first two-fifths of the head-shield in *Altigibbaspis* but at about the midpoint of the head-shield length in *Polybranchiaspis*. The median dorsal ridge in *Altigibbaspis* is high and robust, maintaining nearly constant height along its entire trajectory before sloping down near the posterior margin of the head-shield. By contrast, the median dorsal ridge in *Polybranchiaspis* rises gradually backward along its entire trajectory and finally projects beyond the posterior margin of the head-shield to form a cone-shaped spine.

Description. The new form is a medium-sized polybranchiaspid fish. The head-shield is longitudinally ovoid with a deeply embayed posterior margin. The holotype (V 20843.1) is three-dimensionally preserved, with a maximum length of 62.50 mm (from the rostral margin to the tip of the inner corner), maximum breadth of 52.50 mm, and maximum height of 17.72 mm [Figure 2: see original paper]A–C, [Figure 3: see original paper]A–C. The paratype (V 20843.2) is an incomplete head-shield, with a preserved portion measuring 57.50 mm in maximum length, 49.60 mm in maximum breadth, and 11.35 mm in preserved height [Figure 2: see original paper]D.

On the dorsal side of the head-shield, immediately behind the dorsal commissure (dcm, [Figure 3: see original paper]A, B, D), a robust and high median dorsal ridge (md.r, [Figure 3: see original paper]A–D) rises abruptly along the midline. The ridge extends backward horizontally for about 15.90 mm, then slopes down rapidly as it approaches the posterior margin of the head-shield. The ridge appears hunchback-like in lateral view and becomes blade-like dorsally [Figure 3: see original paper]B. The posterior margin of the head-shield is deeply embayed and bears a short median dorsal spine (md.s, [Figure 3: see original paper]A, B, D) in the middle. The inner corners (ic, [Figure 3: see original paper]A, B, D) are broad and lobate, extending backward well behind the median dorsal spine.

Several sensory organs are visible on the dorsal side of the head-shield. A large median dorsal opening for the nostrils (md.o, Figs. 2, [Figure 3: see original paper]A, B, D) is set in the anterior part of the head-shield. It is transversely oval with a breadth/length ratio of about 2.0. In the holotype, the long and short axes of the median dorsal opening measure 10.97 mm and 5.54 mm respectively, while in the paratype they measure 10.67 mm and 5.75 mm respectively. The length ratio between the median dorsal opening and the head-shield is about 0.10, which is significantly smaller than that of most polybranchiaspids. A pair of orbital openings (orb, [Figure 2: see original paper]A, D, [Figure 3: see original paper]A, B, D) are placed anterodorsally on the head-shield, posterior to the median dorsal opening. The distance between orbital openings is 21.00 mm in the holotype. The orbits are round and medium-sized, with diameters ranging from 4.22 to 5.00 mm in the two specimens. As in most galeaspids (Liu et al., 2014), there is no pineal opening, and the pineal area shows no difference from the surrounding surface.

The sensory canals are exposed as grooves. The sensory canal system displays a typical polybranchiaspid distribution pattern, including the supraorbital system (soc1, soc2, [Figure 3: see original paper]A, B, D), the infraorbital system (ifc, ldc, ltc, [Figure 3: see original paper]A, B, D), and a dorsal commissure (dcm, [Figure 3: see original paper]A, B, D). The supraorbital system consists of anterior and posterior supraorbital canals. The anterior supraorbital canal (soc1, [Figure 3: see original paper]A, B, D) reaches the rostral margin anteriorly and converges posteriorly with the posterior supraorbital canal and the infraorbital canal at the level of the middle of the median dorsal opening. The posterior supraorbital canals (soc2, [Figure 3: see original paper]A, B, D) of both sides converge posteriorly at the level of the posterior end of the orbital opening and are V-shaped. The infraorbital system consists of the infraorbital canal (ifc, [Figure 3: see original paper]A, B, D), the lateral dorsal canal (ldc, [Figure 3: see original paper]A, B, D), and four lateral transverse canals (ltc1-4, [Figure 3: see original paper]A, B, D) issuing from the lateral dorsal canal. The dorsal commissure (dcm, [Figure 3: see original paper]A, B, D) lies in the first two-fifths of the head-shield and connects the lateral dorsal canals of both sides.

The ornamentation is poorly known from polygonal impressions, as the exoskeleton has been weathered away. Each polygonal impression is a natural mold of the basal depression of a tubercle (Tong-Dzuy et al., 1995). The polygonal impressions are large and comparable in size to those of *Polybranchiaspis liaojiaoshanensis*, suggesting that their ornamental tubercles were probably similar in size.

Polybranchiaspidae gen. et sp. indet. ([Figure 4: see original paper])

Referred specimens. A fragmentary head-shield, V 20845.1a, and its external mold, V 20845.1b.

Locality and horizon. Near the northeast entrance of Liaokuo Park, Qujing City, Yunnan Province, China; Xishancun Formation, Early Devonian (early

Lochkovian).

Description. The referred specimens represent part of a head-shield from the posterior margin of the median dorsal opening (md.o, [Figure 4: see original paper]) to the dorsal commissure (dcm, [Figure 4: see original paper]). The long posterior margin of the median dorsal opening suggests that its width was probably much greater than its length. The orbital openings (orb, [Figure 4: see original paper]) are dorsally placed. The anterior supraorbital canals (soc1, [Figure 4: see original paper]) join the posterior supraorbital canals (soc2, [Figure 4: see original paper]), which converge posteriorly at a point just behind the pineal macula (pi.m, [Figure 4: see original paper]) as in most polybranchiaspids. The external mold reveals ornamental tubercles as large as those in some polybranchiaspids such as *Polybranchiaspis* (Liu, 1965, 1975) and *Laxaspis* (Liu, 1975), but with flat rather than pointed tubercle apices as seen in *Polybranchiaspis* and *Laxaspis*. In the new specimen, the distance from the posterior margin of the median dorsal opening to the dorsal commissure is 33.00 mm, which is about the same as that of *L. qujingensis* (32.00 mm) but much smaller than that of *P. liaojiaoshanensis* (21.00 mm).

Order Eugaleaspiformes (Liu, 1965) Liu, 1980
Family Eugaleaspidae (Liu, 1965) Liu, 1980
Genus *Eugaleaspis* (Liu, 1965) Liu, 1980
Species *Eugaleaspis changi* (Liu, 1965) Liu, 1980 ([Figure 5: see original paper])

Galeaspis changi Liu, 1965; Liu, 1975.
Eugaleaspis changi Liu, 1980.

Holotype. A complete head-shield and its natural mold, IVPP V 2981.

Referred specimens. An incomplete head-shield IVPP V 20844.1a and its natural mold V 20844.1b; a fragmentary head-shield V 20844.2a and its natural mold V 20844.2b.

Locality and horizon. Near the northeast entrance of Liaokuo Park, Qujing City, Yunnan Province, China; Xishancun Formation, Early Devonian (early Lochkovian).

Description. Specimen V 20844.1a is an incomplete head-shield with missing corners [Figure 5: see original paper]A, and its natural mold V 20844.1b preserves the posterior margin of the head-shield [Figure 5: see original paper]B. Only a fragment of the left side of the head-shield is preserved in V 20844.2a [Figure 5: see original paper]C and its natural mold V 20844.2b [Figure 5: see original paper]D. Like the holotype of *Eugaleaspis changi*, the new specimens bear a longitudinal, slit-like median dorsal opening about six times longer than broad (md.o, [Figure 5: see original paper]A, E). Other similarities include the distribution pattern of sensory canals and overall size. The anterior supraorbital canals (soc1, [Figure 5: see original paper]A, E) are nearly parallel to the median dorsal opening and do not connect with the posterior supraorbital

canals (soc2, [Figure 5: see original paper]A, E). The head-shield length along the midline is 36.50 mm in V 20844.1a, close to the 37.50 mm of the holotype V 2981 (Liu, 1965). As the galeaspid head-shield is a sutureless carapace, they probably acquired their bony skeleton only at full growth, resulting in a limited size range for each species. The positions of the orbital openings, median dorsal opening, and pineal macula are also identical to those of the holotype. Notably, the so-called "pineal opening" in the holotype described in the original publication (Liu, 1965, 1975) is actually an artificial pore, as a pineal macula does appear in the natural mold of the holotype (Liu et al., 2014).

Order Huananaspiformes Janvier, 1975
Family Nanpanaspidae Liu, 1975

Diagnosis (emended). Head-shield pentagonal in shape, with a rostral process. Corners small, anteriorly placed (lp.a, [Figure 6: see original paper]A, C); the portion of the head-shield posterior to the corner is twice as long as the portion anterior to the corner; the sinus (not, [Figure 6: see original paper]A, C) behind the corner faces laterally and is notch-like along the lateral margin of the head-shield; median dorsal opening longitudinal oval; orbits small, dorsally placed, and close to the midline of the head-shield; branchial fossae about ten or more pairs.

Genus *Nanpanaspis* Liu, 1965
Species *Nanpanaspis microculus* Liu, 1965
Nanpanaspis microculus Liu 1965 ([Figure 6: see original paper])

Holotype. A head-shield lacking the posterior margin and its natural mold, IVPP V 3030.

Referred specimen. A natural mold of a fragmentary head-shield, IVPP V 20846.

Locality and horizon. Near the northeast entrance of Liaokuo Park, Qujing City, Yunnan Province, China; Xishancun Formation, Early Devonian (early Lochkovian).

Description. The new specimen is preserved as a natural mold of the visceral side of the anterior part of the head-shield. As in the holotype of *Nanpanaspis microculus* [Figure 6: see original paper]A, the rostral process (ro, [Figure 6: see original paper]B) of the new material is narrow and short, and the rostral margins on both sides of the head-shield form an angle of about 100°. The new specimen also matches the holotype in having a longitudinal oval median dorsal opening (md.o, [Figure 6: see original paper]A, B) and dorsally placed small orbital openings (orb, [Figure 6: see original paper]A, B).

3.1 Morphological Disparity of Median Dorsal Ridge and Spine in Galeaspids

The median dorsal ridge (md.r, [Figure 7: see original paper]A–C) is widely present in galeaspids except eugaleaspidiforms and can be morphologically classified into three types [Figure 7: see original paper]. In the first type, the ridge (md.r, [Figure 7: see original paper]A) begins just behind the dorsal commissure, rises gradually, and projects beyond the posterior margin of the head-shield to form a cone-shaped spine (md.s, [Figure 7: see original paper]A). This type is common in *Hanyangaspis* (Pan, 1986, dsp:fig. 3A), many polybranchiaspids such as *Polybranchiaspis* (Liu, 1975, d.sp:fig. 5), *Laxaspis* (Liu, 1975, d.sp:fig. 6), *Damaspis* (Wang and Wang, 1982a, dsp:fig. 1), and most huananaspids such as *Huananaspis* (Liu, 1973:fig. 3), *Sanchaspis* (Pan and Wang, 1981:fig.1), and *Antiquisattiaspis* (Liu, 1985:fig. 1). In the second type, the median dorsal ridge (md.r, [Figure 7: see original paper]B) also begins just behind the dorsal commissure but rises steeply to form a high, upright, and compressed spine (md.s, [Figure 7: see original paper]B). This type is found only in two forms: *Siyingia altuspinosa* [Figure 7: see original paper]B (Wang and Wang, 1982b) and *Hyperaspis acclivis* (Pan, 1992:fig. 35). In the third type, exemplified by *Altigibbaspis*, the median dorsal ridge (md.r, [Figure 7: see original paper]C) is blade-like, maintaining nearly constant height along its entire trajectory before sloping down close to the posterior margin of the head-shield.

Most galeaspids were bottom-dwellers on sandy or muddy substrates in marginal marine environments (Janvier, 1996; Gai et al., 2015). The median dorsal ridge probably provided hydrodynamic stability in moderate currents at low energetic cost, functionally analogous to the vertical stabilizer of an aircraft. The morphological disparity of median dorsal ridges and spines likely indicates additional functions evolved in galeaspids. Considering the large aquatic predatory sea scorpions (eurypterids) from the Xishancun Formation (cover image)—for example, a huge claw of Pterygotidae gen. et sp. indet., which was erroneously reported as coming from the Xitun Formation in its original description (Wang and Gai, 2014)—we suggest that a high, upright, and compressed spine may have made galeaspid fishes appear larger to predators (Janvier, 1996), while a blade-like median dorsal ridge may have provided defense against sea scorpion claws.

3.2 The Phylogenetic Position of *Nanpanaspis*

The phylogenetic position of *Nanpanaspis* has long been debated. When *Nanpanaspis* was erected (Liu, 1965), its family and order were left indeterminate. Liu (1975) proposed the family Nanpanaspidae and order Nanpanaspiformes for the genus. Janvier (1975) tentatively assigned *Nanpanaspis* to an indeterminate family of the Polybranchiaspiformes, while Zhu and Gai (2006) regarded it as the sister taxon of *Asiaspis* within the Huananaspidae.

The controversy stems partly from different interpretations of certain structures

in *Nanpanaspis*. The head-shield of *Nanpanaspis* is roughly pentagonal with a slender, pointed rostral process. Compared to other galeaspids, *Nanpanaspis* is peculiar in bearing two short, laterally projecting processes (lp.a, lp.p, [Figure 6: see original paper]C) with a notch (not, [Figure 6: see original paper]C) between them. Zhu and Gai (2006) suggested that the anterior and posterior lateral processes are homologous with the corner and inner corner of the Huananaspidae, respectively (c, ic, [Figure 8: see original paper]A). However, compared to the laterally projecting corner of the Huananaspidae, the anterior process of *Nanpanaspis* is positioned more anteriorly, near the level of the orbital opening (orb, [Figure 8: see original paper]A). Its posterior process projects laterally, whereas the inner corner in the Huananaspidae projects posteriorly. Therefore, the homology between the two processes of *Nanpanaspis* and the corner and inner corner of the Huananaspidae is not convincingly established.

If the two processes are merely considered a by-product of the marginal notch without any homology to the corner and inner corner of other galeaspids, *Nanpanaspis* would resemble *Gumuaspis* in possessing a rostral process and lacking corners (Wang and Wang, 1992) and should be referred to the Polybranchiaspiformes [Figure 8: see original paper]B.

Another possibility is that the anterior and posterior lateral processes of *Nanpanaspis* are comparable to the orbital process and laterally projecting corner of *Lungmenshanaspis*, respectively, and the notch is comparable to the concave lateral margin of the head-shield in *Lungmenshanaspis* (P' an et al., 1975; Wang et al., 1996). *Lungmenshanaspis*, whose type species is *L. kiangyouensis* [Figure 8: see original paper]C, middle, was referred to the Huananaspidae (P' an et al., 1975). A prominent process (or.p, [Figure 8: see original paper]C) is set along the lateral margin of the head-shield at the level of the orbital openings (orb, [Figure 8: see original paper]C) in *Lungmenshanaspis*, while the margin from the process to the corner of the head-shield is deeply concave (not, [Figure 8: see original paper]C). Based on this outline, Wang (1991) speculated that a lateral fenestra existed on each side of the head-shield as in *Qingmenaspis* (Pan and Wang, 1981:fig. 3) and concluded that the orbital process and concave margin were artificial structures caused by breakage of the lateral margin of the fenestra.

Wang et al. (1996) described another species of *Lungmenshanaspis*, *L. yunnanensis* [Figure 8: see original paper]C, left, whose prominent orbital process (or.p, [Figure 8: see original paper]C) and concave margin (not, [Figure 8: see original paper]C) are strikingly similar to those of *L. kiangyouensis* [Figure 8: see original paper]C, middle. The excellent preservation of *L. yunnanensis* indicates that the orbital process and concave margin are natural structures, particularly since the concave margin bears denticles that continue into the corner (Wang et al., 1996). Consequently, the so-called "lateral fenestra" does not exist in *Lungmenshanaspis*. The anterior process (or.p, [Figure 8: see original paper]C) of *Nanpanaspis* is strikingly similar to the orbital process of *Lungmenshanaspis* in its small size and anterior position level with the orbital opening (orb, [Figure

8: see original paper]C). If this homology holds, *Nanpanaspis* could be resolved as a close relative of *Lungmenshanaspis* within the Huananaspiformes [Figure 8: see original paper]C.

Considering the three possibilities above, we tend to accept the homology of the anterior process of *Nanpanaspis* with the corner of the Huananaspidae but doubt the homology of the posterior process with the inner corner, as the inner corner in the Huananaspidae is typically positioned behind the level of the posterior margin of the head-shield and projects caudally. The notch between the anterior and posterior processes is probably comparable to the armpit-like sinus of other galeaspids such as *Kwangnanaspis subtriangularis* (Cao, 1979:fig. 1; Liu et al., 2015:fig. 99) and *Eugaleaspis xujiachongensis* (Liu, 1975:fig.2; Liu et al., 2015:fig. 89). Given the unique morphology of *Nanpanaspis*, which is difficult to compare with other galeaspids, and its early occurrence among the Huananaspiformes, we assign *Nanpanaspis* to the monogeneric family Nanpanaspidae, which provisionally represents an early branch of the Huananaspiformes [Figure 8: see original paper]D.

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Note: Figure translations are in progress. See original paper for figures.