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A new species of *Siyingia* from the Lower Devonian Xishancun Formation of Qujing, Yunnan

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Abstract This paper describes a new species of the Polybranchiaspiformes (Agnatha: Galeaspida), *Siyingia perlatuspinosa* sp. nov., from the Early Devonian Xishancun Formation in Qujing, East Yunnan, southwestern China. The diagnosis of the genus *Siyingia* is emended based on data from the holotype of the new species. A phylogenetic analysis, using an expanded version of the data matrix of Zhu and Gai defined in 2006, suggests that *Siyingia* and *Polybranchiaspis* form the monophyletic sister group of a clade containing *Laxaspis* and *Damaspis*. This discovery increases the known Early Devonian diversity of polybranchiaspiforms, and helps to clarify the pattern of interrelationships within the Polybranchiaspiformes.

Key words Qujing, Yunnan, China; Early Devonian; Xishancun Formation; Polybranchiaspiformes, *Siyingia*

1 Introdution

A continuous fossiliferous Lower Devonian succession, comprising in ascending order the Xishancun, Xitun, Guijiatun and Xujiachong formations, is well exposed in the Paleozoic Qujing Basin in eastern Yunnan (Fig. 1(a)). The Qujing Basin has been interpreted as representing an intercontinental marginal fault basin with both gulf and tidal flat depositional environments (Zheng and Zhang, 1989; Dong, 1992; Zeng et al., 1992; Fan and Liu, 1995; Shan and Wang, 2000). The Xishancun Formation mainly comprises gray-yellow sandstone and siltstone intercalated with silty shale (Fang et al., 1985). The formation contains an abundant fossil fish fauna in which the jawless galeaspids, and particularly members of the galeaspid clade Polybranchiaspiformes, are well-represented and diverse (Fig. 1(b)). In addition, there are many antiarchs, arthrodires, petalichthyids, sarcopterygians, and microvertebrate remains, including those of thelodonts, together with plants and invertebrates (Liu, 1965, 1975; P'an and Wang, 1978; Wang and Dong, 1989; Wang, 1995a, b; Wang, 2000; Zhu and Schultze, 1997; Gai and Zhu, 2007; Zhao and Zhu, 2010).

Galeaspids from the Xishancun Formation that have been documented to date include:

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the Eugaleaspiformes *Eugaleaspis changi* (Liu, 1965, 1975), *Yunnanogaleaspis major* (Pan and Wang, 1980), and *Nochelaspis maeandrine* (Zhu, 1992); the Polybranchiaspiformes *Polybranchiaspis liaojiaoshanensis* (Liu, 1965, 1975), *P. minor* (Liu, 1975), *P. miandiancunensis*

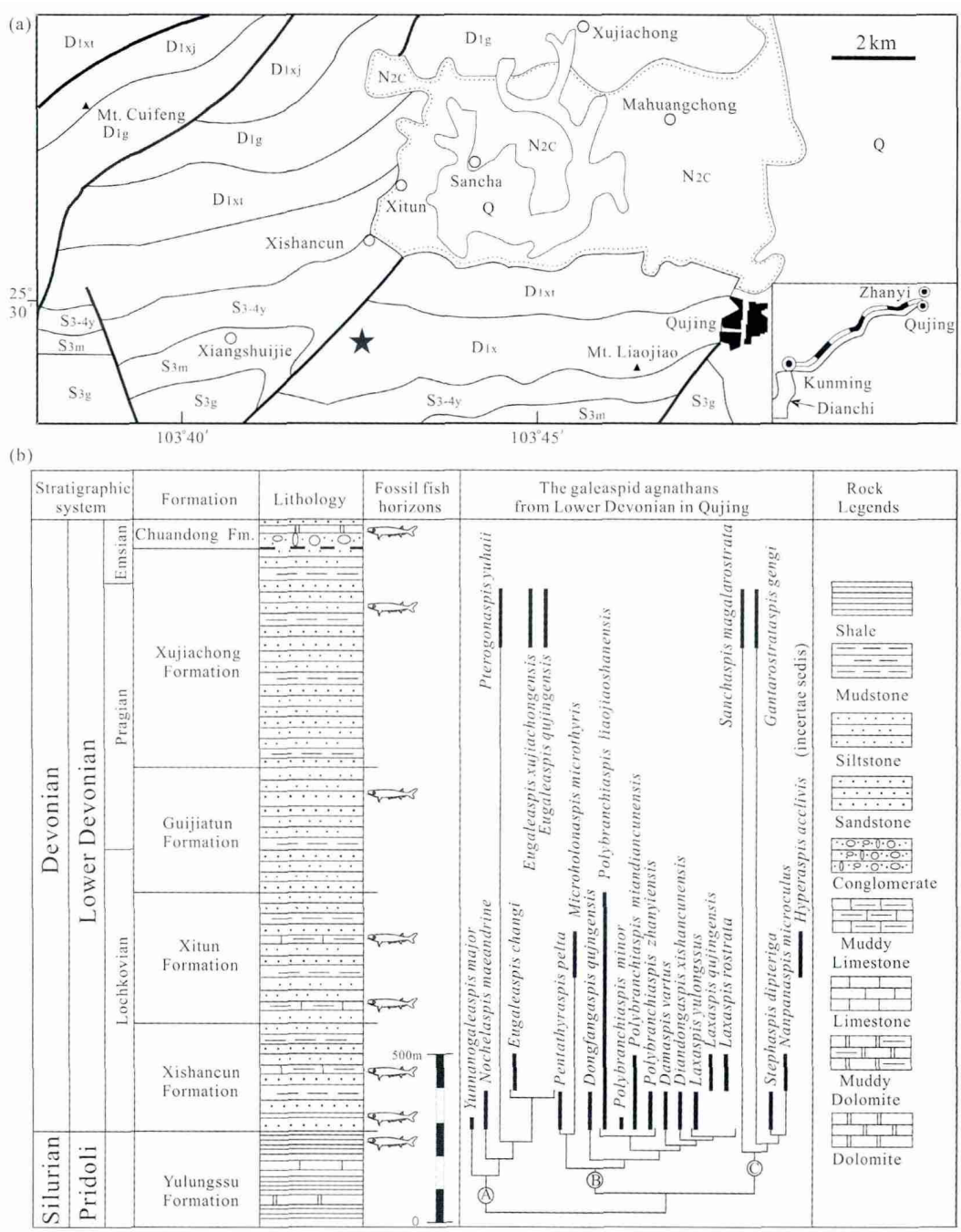

Fig. 1 Geological map (a) and columnar section (b) of Lower Devonian in Qujing of eastern Yunnan
★ site where the holotype of *Siyingia perlatuspinosa* sp. nov. was discovered; A–C. nodes corresponding to Eugaleaspiformes, Polybranchiaspiformes and Huananaspiformes, respectively

(P'an and Wang, 1978), *P. zhanyiensis* (P'an and Wang, 1978), *Laxaspis qujingensis* (Liu, 1975), *L. yulongssus* (Liu, 1975; Zhu and Gai, 2006), *L. rostrata* (Liu, 1975), *Diandongaspis xishancunensis* (Liu, 1975), *Damaspis vartus* (Wang and Wang, 1982a), *Dongfangaspis qujingensis* (Pan and Wang, 1981; Pan, 1992), and *Pentathyras pelta* (Pan, 1992); and the Huananaspiformes: *Nanpanaspis microculus* (Liu, 1965) and *Stephaspis dipteriga* (Gai and Zhu, 2007) (Fig. 1(b)). Among these known galeaspids, *Eugaleaspis changi*, *Nanpanaspis microculus*, *Laxaspis qujingensis* and *L. rostrata* were originally reported to have come from the Xitun Formation (Liu, 1965, 1975). In fact, all of them were excavated from the middle part of the Xishancun Formation. Therefore, we include them in the list of the galeaspids known from the Xishancun Formation in this paper. The fossil fishes from the Xishancun Formation (Qujing, Yunnan), document the first radiation of galeaspids during the Devonian in China (Zhao and Zhu, 2007).

In the present paper, we describe a new polybranchiaspiform galeaspid, *Siyingia perlatuspinosa* sp. nov., from the Lower Devonian Xishancun Formation in Qujing. The new species is very similar to the type species of *Siyingia*, *S. altuspinosa* from Siying, Yiliang County (Wang and Wang, 1982b), but differs from *S. altuspinosa* in that the median dorsal spine extending from the posterodorsal part of the headshield is broad rather than high and laterally compressed. The discovery of *S. perlatuspinosa* in the Qujing area increases the Early Devonian diversity of polybranchiaspiforms, and the new specimen also provides some evidence that helps to clarify the pattern of interrelationships within the Polybranchiaspiformes.

2 Systematic paleontology

Subclass Galeaspida Tarlo, 1967

Supraorder Polybranchiaspidida Janvier, 1996

Order Polybranchiaspiformes Liu, 1965

Family Polybranchiaspidae Liu, 1965

Genus *Siyingia* Wang & Wang, 1982

Type species *Siyingia altuspinosa* Wang & Wang, 1982.

Etymology After the fossil locality Siying in Yiliang, Yunnan Province, China.

Diagnosis (emended) Medium-sized polybranchiaspid with ovoid headshield whose length is almost equal to its width; high and well-developed dorsal spine extending from posterodorsal part of headshield; median dorsal opening elliptical, with short axis aligned anteroposteriorly; orbits round, medium-sized, and dorsally placed; sensory canal system displaying typical polybranchiaspid pattern; dorsal commissure located almost in middle of headshield; anterior margin of oral opening with inverted V-shape, and located on rostroventral margin of headshield; and ornament of the headshield comprises minute, uniformly distributed polygonal tubercles.

Remarks The type species of *Siyingia* (Wang and Wang, 1982b), *S. altuspinosa*, was erected based on an incomplete external mold of a headshield collected from the Lower

Devonian Xitun Formation. *Siyingia* is very similar to *Polybranchiaspis* and *Diandongaspis* in the shape of the headshield, the relative positions of the median dorsal opening and orbital openings, and the layout of the sensory canal system. Nevertheless, some clear differences among these genera exist. Firstly, *Siyingia* possesses an especially high median dorsal spine. The median dorsal spine is well-developed in polybranchiaspids, such as *Polybranchiaspis*, *Laxaspis*, *Diandongaspis*, and *Damaspis*. The median dorsal spine of *Siyingia* is high, rather than low and flat as *Polybranchiaspis* and *Diandongaspis*. Median dorsal spine morphology should be regarded as an important and meaningful basis for classification within the polybranchiaspiforms. Secondly, the end of the median dorsal spine and the posterior margin of the inner corners of *Siyingia* are placed almost at a same vertical plane, in strong contrast to the condition in the other polybranchiaspids. Thirdly, the anterior margin of the oral opening has an inverted "V" shape in *Siyingia*, differing clearly in morphology from the equivalent structure in *Polybranchiaspis* and *Diandongaspis*. Therefore, *Siyingia* can be regarded as a valid genus of Polybranchiaspiformes.

***Siyingia perlatuspinosa* sp. nov.**

(Figs. 2−4)

Etymology From *perlatus* (Latin), very broad; *spinos* (Latin), spinous.

Holotype IVPP V 13771.1a, b, an incomplete headshield and its external mold.

Locality and horizon Lochkovian, Lower Devonian, Xishancun Formation, Qujing, Yunnan, China.

Diagnosis Medium-sized polybranchiaspid with high, broad (ratio of maximum breadth to maximum length around 2.0) and well-developed median dorsal spine extending from the posterior part of headshield, immediately behind dorsal commissure; sensory canals without biramous ends and displaying typical polybranchiaspid pattern; inner corners broad and leaf-shaped; and 12 pairs of closely set branchial fossae present, and slightly anterodorsally inclined.

Remarks The new specimen, collected from the middle part of the Xishancun Formation in Qujing, strikingly resembles the type species *Siyingia altuspinosa* in having a high median dorsal spine that is just posterior to the median dorsal commissure, a sensory canal system arranged in a typical polybranchiaspid pattern, flat-topped polygonal tubercles, and a medium-sized headshield whose length and width are almost equal. Thus, the new specimen can be definitively referred to the genus *Siyingia*. However, the new specimen differs from the type species in the structure of the median dorsal spine and the ends of the sensory canals. Although the median dorsal spine is as high as that of *S. altuspinosa*, it is broad rather than laterally compressed. In addition, the sensory canals of the new form have simple unbranched ends, rather than forking ones as in *S. altuspinosa*. Re-examination of the holotype of *S. altuspinosa* suggests that some important features (e.g. the pineal opening, inner corners, and branchial fossae) are not preserved, reducing the value of the original diagnosis of the

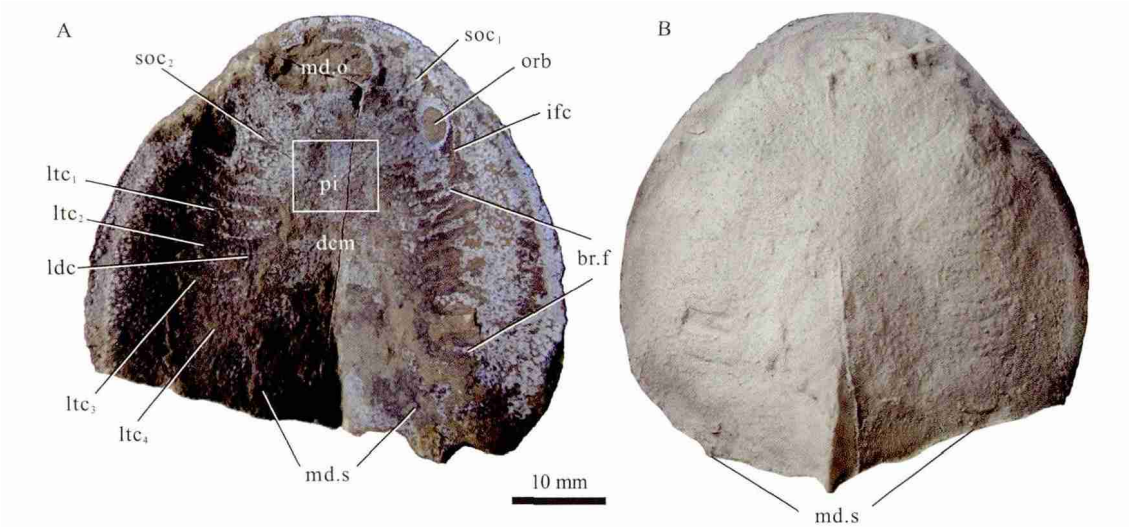

Fig. 2 Photographs of an external mold of the headshield (A) and its silicone rubber cast in dorsal view (B) of the holotype of *Siyingia perlatuspinosa* sp. nov. (IVPP V 13771.1b, c)
Box in (A) indicates region shown in detail in Fig. 3C
Abbreviations: br.f. branchial fossa 鳃穴; dcm. dorsal commissure 背联络管; ifc. infraorbital canal 眶下管; ldc. lateral dorsal canal 侧背管; ltc_{1-4}. first to fourth lateral transverse canal 第1至第4侧横管; md.o. median dorsal opening 中背孔; md.s. median dorsal spine 中背棘; orb. orbital opening 眶孔; pi. pineal opening 松果孔; soc_1. anterior supraorbital canal 前眶上管; soc_2. posterior supraorbital canal 后眶上管

genus. Our new specimen of *Siyingia* will help to clarify the morphological characters present in genus.

Description External morphology: the type specimen (IVPP V 13771.1a, b), including an incomplete headshield (V 13771.1a) and its external mold (V 13771.1b), is the only material of *Siyingia perlatuspinosa* (Figs. 2A, 3A, B). The right inner corner in the external mold of the headshield (V 13771.1b) is slightly damaged, but the left one is almost completely preserved in the headshield (V 13771.1a). The rostral margin of the headshield is not complete, and the end of the median dorsal spine is well preserved but slightly distorted (Fig. 3A, B).

The headshield is generally ovoid, being very slightly longer than the broad. The preserved maximum length of the headshield is 58.7 mm. The shield reaches its maximum breadth of 58.6 mm near its anteroposterior midpoint, approximately at the level of the ends of the second pair of lateral transverse canals. The rostral margin of the headshield is semicircular, and lacks a protruding rostral process. The headshield is dorsally convex in both the transverse and anteroposterior views, forming a domed structure whose apex is situated at the posterior end of the median dorsal spine.

The median dorsal opening (md.o, Fig. 2A) is situated on the anterodorsal surface of the headshield, and is transversally elongated and subelliptical as in other polybranchiaspids. This opening is about 6.7 mm long and 14.3 mm wide, resulting in a length/width ratio of 1:2.1. The distance from the anterior margin of the median dorsal opening to the rostral end of the headshield is about 4.4 mm, whereas the distance from the posterior margin of the median

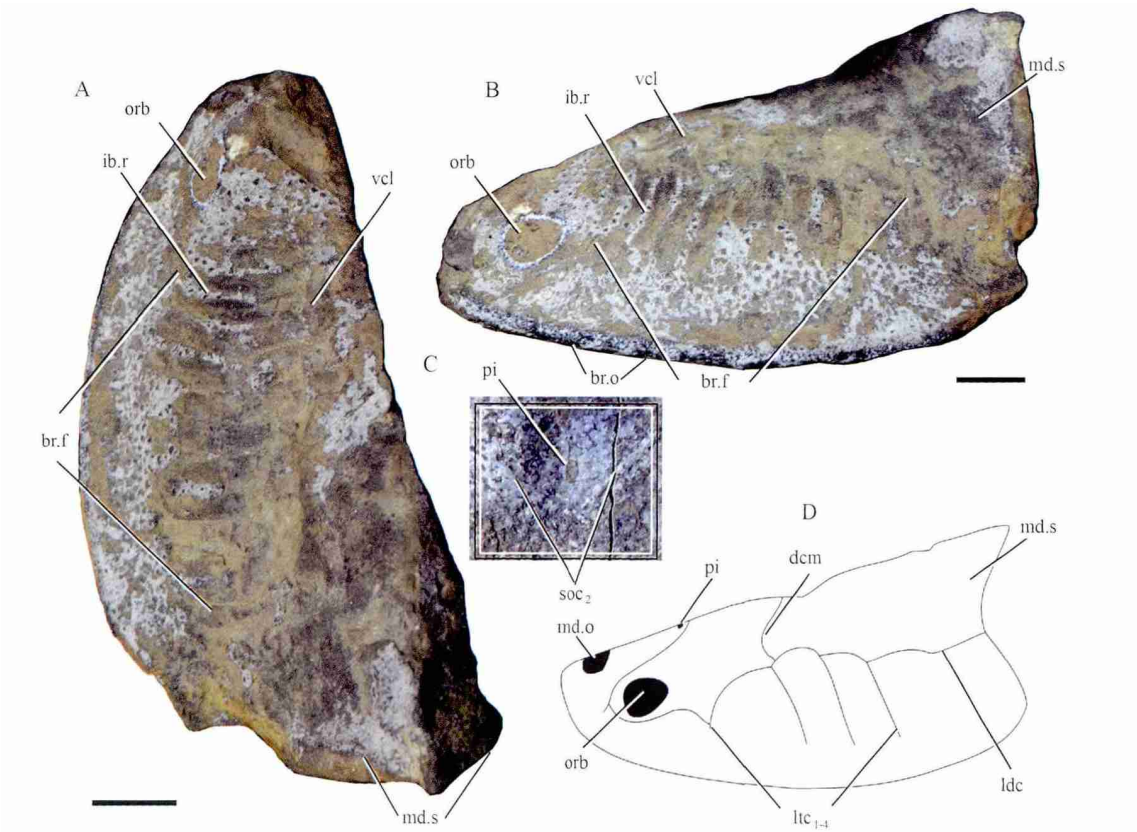

Fig. 3 Incomplete headshield of the holotype of *Siyingia perlatuspinosa* sp. nov. (IVPP V 13771.1a)
A. dorsal view; B. lateral view; C. close-up of vicinity of pineal opening (region indicated by box in Fig. 2A); D. line drawing, in lateral view; scale bars equal 5 mm
Abbreviations: br.o. branchial opening 鳃孔; ib.r. interbranchial ridge 鳃间脊; vcl. canal for the lateral head vein (vena capitis lateralis) or dorsal jugular vein 头侧静脉或背颈静脉; other abbreviations as in Fig. 2

dorsal opening to the level of the anterior margins of orbital openings is about 7.7 mm.

The orbital openings (orb, Figs. 2A, 3A, B) are nearly round, and are of moderate size, with a maximum diameter of 4.2 mm. They are situated anterodorsally, but posterior to the median dorsal opening, and the distance between the two orbital openings is about 24.5 mm.

The relatively large pineal opening (pi, Fig. 2A) is situated posterior to the median dorsal opening and the posterior margins of the orbital openings. It has the shape of longitudinally elongated oval, with the long axis measuring 1.9 mm and the short axis measuring 1.3 mm. The anterior margin of the pineal opening is about 19.1 mm from the rostral end of the headshield, and the posterior margin of the opening is about 32.8 mm from the caudal end. The pineal opening, like the median dorsal opening and orbital openings, pierces through the dorsal shield.

A well-developed median dorsal spine (md.s, Figs. 2A, 3A, B) extends posterodorsally, immediately behind the dorsal commissure that occupies a central position on the headshield. The maximum breadth and height of the spine, or the maximum width of its base and the

vertical distance between its end and base, are about 32.8 and 16.7 mm respectively, resulting in a ratio of maximum breadth to maximum height of around 2.0.

Based on the almost complete inner corner seen in the left headshield, with a preserved natural edge (Figs. 2A, 3A, B), it is clear that the inner corners are broad and leaf-shaped in form. The posterior margins of the inner corners are at the same level as the end of the median dorsal spine.

The well-preserved sensory canal system displays a typical polybranchiaspid pattern and includes supraorbital systems, infraorbital systems, and a median dorsal commissure (Figs. 2A, 4A, B). The sensory canals all terminate in unbranched ends, in contrast to the condition in the type species *Siyingia altuspinosa* (Wang and Wang, 1982b). The supraorbital systems consist of a pair of anterior supraorbital canals (soc_1) and a pair of posterior supraorbital canals (soc_2). The anterior supraorbital canals are close to the anterior margin of the shield, and extend posteriorly and laterally. Each anterior supraorbital canal meets the posterior supraorbital canal and infraorbital canal (ifc) directly above the orbital opening, forming a triple junction. The left and right posterior supraorbital canals (soc_2, Figs. 2A, 3C, 4) converge at a point just behind the pineal opening, forming a broad V-shape. The infraorbital systems include one infraorbital canal (ifc), one lateral dorsal canal (ldc), and four lateral transverse canals (ltc_{1-4}) on each side of the dorsal headshield. The infraorbital canal starts at the triple junction mentioned above, extends posteriorly and bypasses the lateral margin of the orbital opening in a sigmoid curve, and finally intersects with the first lateral transverse canal (ltc_1). The lateral dorsal canal extends posteriorly to the posterior margin of the headshield, and gives rise to four lateral transverse canals on each side. The first lateral transverse canal extends anterolaterally, forming an angle of 25° with the transverse axis. The other three lateral transverse canals extend posterolaterally at an angle of 20°. The single median dorsal commissure (dcm) is located almost in the middle of the headshield. This structure connects the two lateral dorsal canals at the level of the second pair of lateral transverse canals.

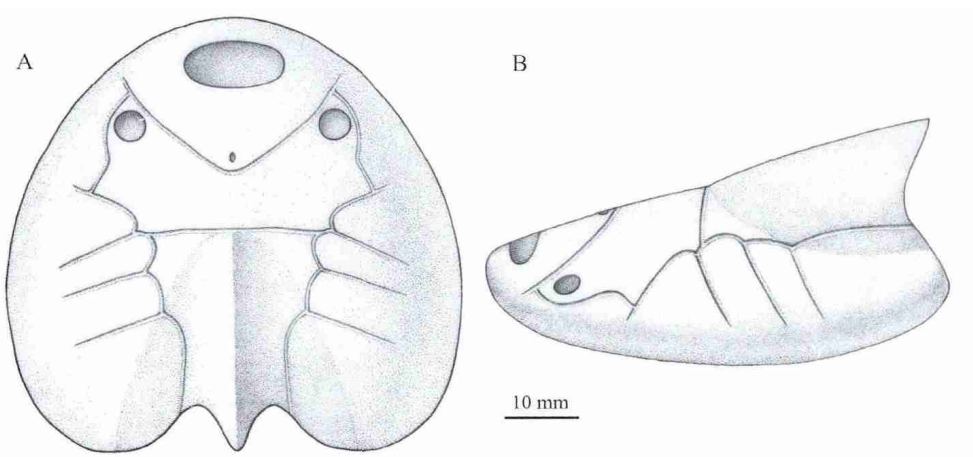

Fig. 4 Restoration of the headshield of *Siyingia perlatuspinosa* sp. nov.
A. dorsal view; B. lateral view

The exoskeleton is ornamented with minute, polygonal, flat-topped tubercles. They are evenly distributed on the surface of the headshield and there are 4-6 tubercles in every square millimeter.

Internal structure: in the holotype IVPP V 13771.1a, the branchial fossae (br.f, Fig. 3A, B) and the left canal for the lateral head vein (vena capitis lateralis) or dorsal jugular vein (vcl, Fig. 3A, B) are completely and distinctly preserved. Unlike in the exquisitely preserved *Duyunolepis paoyangensis* and *Paraduyunaspis hezhangensis*, however, the endocranium and central nervous system cannot be observed.

The 12 pairs of branchial fossae occupy most of the headshield (Figs. 2A, 3A, B), a condition similar to that seen in *Polybranchiaspis liaojiaoshanensis* (which has at least 11 pairs). The branchial fossae are narrow, closely set, and separated by very thin interbranchial ridges (ib.r, Fig. 3A, B). There are about five branchial fossae within 10 mm range. Each branchial fossa extends anterolaterally with an upward-sloping curve and possesses a branchial opening (br.o, Fig. 3B) in its end which are visible in V 13771.1a. The angle between the long axis of each brachial fossa and the midline of the headshield is about 70° in anterior part of the headshield, and 80° in the posterior part. The branchial fossae in the middle are longer than those in the front and rear. In the new species, the longest branchial fossa measures about 15.8 mm, and the shortest around 6.4 mm.

A long tube-like sinus close to the inner ends of the left branchial fossae of V 13771.1a (Fig. 3A, B) probably represents the canal for the lateral head vein (vena capitis lateralis) or dorsal jugular vein (vcl). This structure is visible between the levels of the first and last branchial fossae.

3 Phylogenetic analysis

With the benefit of the new fossil data, we explored the phylogenetic position of *Siyingia* and attempted to clarify the pattern of phylogenetic interrelationships within the Polybranchiaspiformes. We compiled a data set of 54 characters and 40 taxa, primarily based on the earlier data set of Zhu and Gai (2006).

In the new species of *Siyingia*, the headshield is widest near its anteroposterior midpoint as in *Polybranchiaspis* and *Dongfangaspis*. This differs from the condition in the polybranchiaspids *Laxaspis* and *Damaspis*, in which the headshield clearly reaches its maximum width in the posterior part. This difference in the position of the maximum width of the headshield seems likely to be one of the most taxonomically important morphological features among polybranchiaspids. Accordingly, a new morphological character (Character 54) was included in the new data matrix compiled for this study. The formulation of the character is as follows.

Character 54: Position of the maximum width of the ovoid headshield. (0) Approximately in the middle of the headshield, (1) Clearly in the posterior part of the headshield.

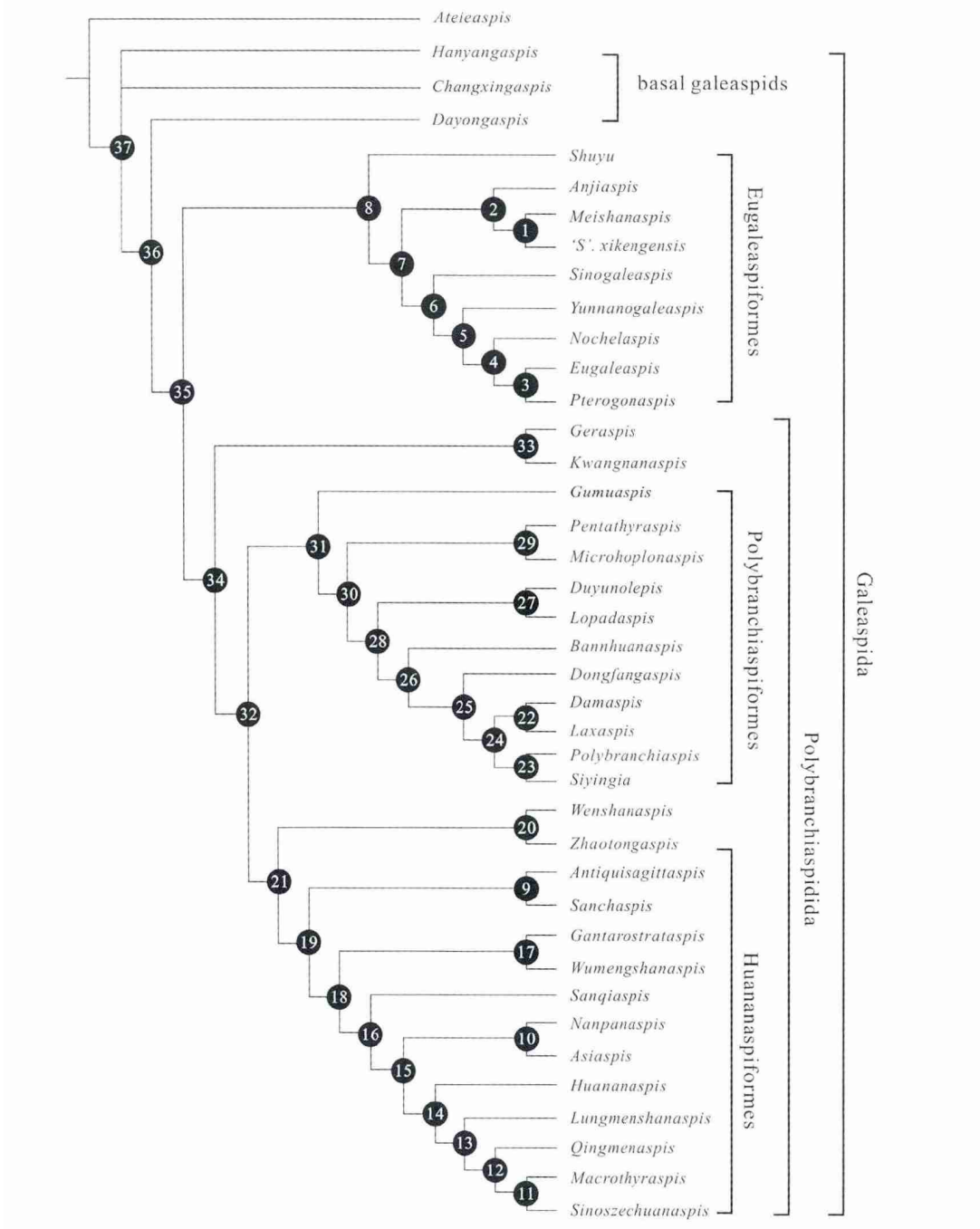

Fig. 5 Strict consensus tree recovered in the phylogenetic analysis

Characters supporting numbered nodes within the order Polybranchiaspiformes are as follows: Node 22: 51(1), 54(1); Node 23: 33(0); Node 24: 43(1); Node 25: 31(1); Node 26: 35(0), 37(0); Node 27: 19(1), 49(2); Node 28: 33(1), 40(1); Node 29: 25(1); Node 30: 4(2); Node 31: 14(0), 50(1). Please see analysis and character descriptions in Zhu and Gai (2006) for characters supporting other nodes

The phylogenetic analysis included 39 galeaspid genera as ingroup taxa. The basal osteostracan genus *Ateleaspis* was selected as outgroup for the analysis, which was performed using PAUP 4.0b10, cladistics package (Swofford, 1993). In the calculation, we used heuristic tree search option, with all characters assigned equal weights and unordered.

The maximum parsimony analysis recovered three most parsimonious trees (MPT) of length 129, with a consistency index (CI) of 0.5039 and a retention index (RI) of 0.7994. The results of the parsimony analysis are basically identical to those of the analysis by Zhu and Gai (2006). The strict consensus tree arising from three most parsimonious trees recovered in the present analysis is shown in the following (Fig. 5).

In all three most parsimonious trees, the close relationship between *Siyingia* and *Polybranchiaspis* is obviously supported by the presence in both taxa of a sensory canal system in which the canals have unbranched ends, a synapomorphic feature (Node 23, Fig. 5). Unlike the small median dorsal spine on the headshield of *Polybranchiaspis*, the median dorsal spine of *Siyingia* is large and broad. The monophyletic group formed by *Siyingia* and *Polybranchiaspis* (Node 23, Fig. 5) is the sister group of *Laxaspis*+*Damaspis* (Node 22, Fig. 5), which is diagnosed by characters including a headshield width/length ratio larger than 1.0 and the fact that the ovoid headshield reaches its maximum width in its posterior part (Node 22, Fig. 5).

These two monophyletic groups, together with the genera *Dongfangaspis* and *Bannhuanaspis*, form the clade Polybranchiaspidae (Node 26, Fig. 5). Besides the Polybranchiaspidae, the Polybranchiaspiformes includes two other monophyletic groups containing multiple genera [Duyunolepidae (Node 27, Fig. 5) and Pentathyraspidae (Node 29, Fig. 5)], in addition to the basally positioned genus *Gumuaspis*.

4 Discussion

The polybranchiaspiforms existed from the Lochkovian (Early Devonian) to the Eifelian (Middle Devonian), and are a highly diverse group of jawless galeaspids. Polybranchiaspiformes currently includes 25 species referred to 16 genera, and the group is endemic to South China and North Vietnam. The 16 described polybranchiaspiform genera are *Gumuaspis*, *Pentathyraspis*, *Microhoplonaspis*, *Duyunolepis*, *Paraduyunaspis*, *Neoduyunaspis*, *Lopadaspis*, *Bannhuanaspis*, *Clarorbis*, *Dongfangaspis*, *Polybranchiaspis*, *Siyingia*, *Laxaspis*, *Damaspis*, *Diandongaspis*, and *Cyclodiscaspis*, and the last nine of these are assigned to the family Polybranchiaspidae (Fig. 6).

The genus *Clarorbis* includes the single species *C. apponomedianus* from the Eifelian of southeast Guangxi (Pan and Ji, 1993). This species resembles *Bannhuanaspis vukhuci* in that many lateral transverse canals branch from the infraorbital canal, and in having an ornamentation comprising tiny round tubercles (Janvier et al., 1993; Zhu and Gai, 2006). *C. apponomedianus* and *B. vukhuci* form a clade that occupies the most basal position within

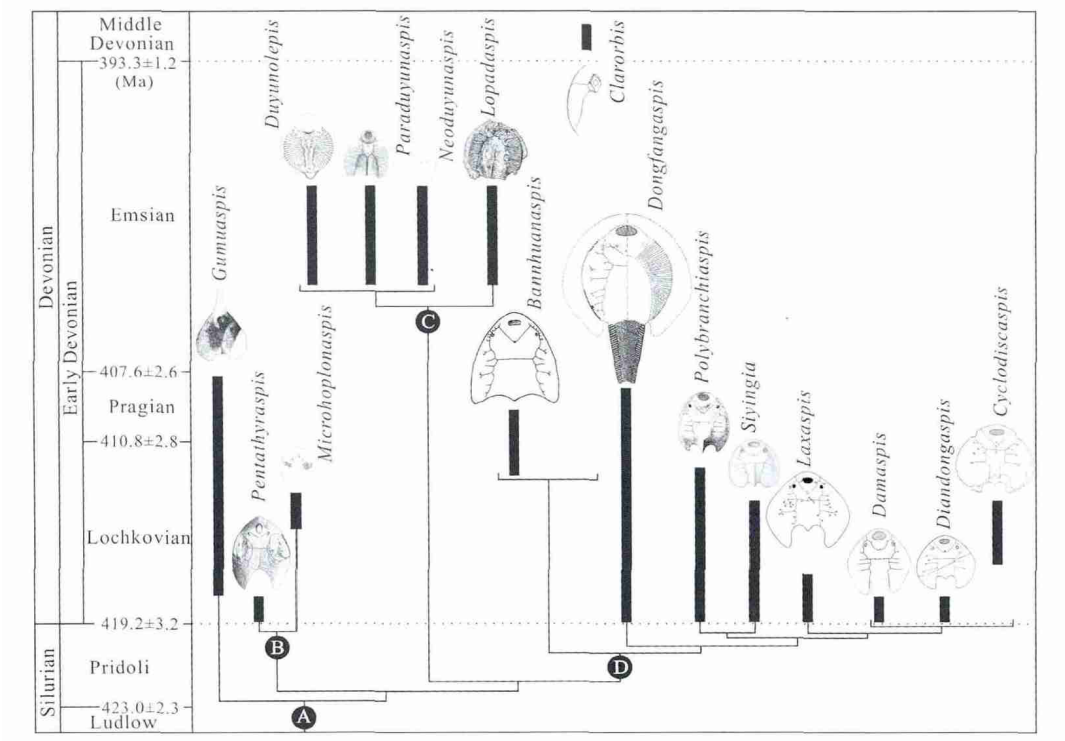

Fig. 6 Temporal distribution of the polybranchiaspiforms

Slim lines indicate polybranchiaspiform interrelationships; Node A: Polybranchiaspifomes; Node B: Pentathyraspidae; Node C: Duyunolepidae; Node D: Polybranchiaspidae

the family Polybranchiaspidae (Node D, Fig. 6). In general, basal groups should occur in older strata. However, phylogenetic relationships within the family Polybranchiaspidae are inconsistent in this respect with the fossil record as it is currently known. The condition is the same as the genus *Gumuaspis* occupying the most basal position in the order Polybranchiaspifomes. Therefore, future excavations in South China and North Vietnam should reveal basal polybranchiaspiforms or polybranchiaspids in older strata.

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云南曲靖下泥盆统西山村组四营鱼属(*Siyingia*)一新种

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摘要：主要采用形态学与比较解剖学的方法，对采自云南曲靖地区下泥盆统西山村组中的1件盔甲鱼类标本进行了详细的形态学研究，建立了多鳃鱼类四营鱼属1新种：宽棘四营鱼(*Siyingia perlatuspinosa* sp. nov.), 并据此修订了四营鱼属的特征。在此基础上，应用分支系统学对多鳃鱼类属一级的系统发育关系进行了重新分析与探讨，确定了四营鱼在多鳃鱼类中的系统发育位置。系统发育分析结果显示，四营鱼(*Siyingia*)与多鳃鱼(*Polybranchiaspis*)亲缘关系最近，二者形成了一个单系类群，与宽甲鱼(*Laxaspis*)+坝鱼(*Damaspis*)组成的单系类群互为姊妹群。宽棘四营鱼的发现不仅拓宽了四营鱼在华南的时空分布范围，而且丰富了多鳃鱼类的多样性，并为多鳃鱼类的深入研究提供了可靠的化石新证据。

关键词：云南曲靖，早泥盆世，西山村组，多鳃鱼类，四营鱼

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